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BIOLOGICAL INVESTIGATIONS OF THE DEEP SEA. 47.
A MONOGRAPH OF THE CEPHALOPODA OF
THE NORTH ATLANTIC.
THE FAMILY HISTIOTEUTHIDAE¹

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ABSTRACT

The worldwide mesopelagic squids of the family Histioteuthidae are revised. A single genus, *Histioteuthis*, is recognized and redefined. Three new species, *eltaninae*, *macrohista*, and *bruuni*, and one new subspecies, *corona berryi*, are described. Neotypes are named for *miranda* (Berry, 1918) and *meleagroteuthis* (Chun, 1910), and the validity of Hoyle's (1885) species *atlantica* is confirmed. A comprehensive historical résumé and taxonomic discussion of the general morphology of the family are given as well as a key to the 13 recognized species. Each species is fully described and illustrated, and synonymies and distributions are given. *Species dubia*, published misidentified species, and museum names occurring in the family are discussed.

INTRODUCTION

The histioteuthids have always attracted attention by their beauty and unique appearance, but have long confused workers because of the seeming lack of stability in taxonomic characters which was due in considerable degree to scarcity of comparative material. For some time, histioteuthids have been known to be one of the important items in the diet of certain whales, and with the increased appearance of the group in the current growing study of the midocean waters, the necessity for the present work has been emphasized.

When the excellent DANA collection of primarily postlarval and juvenile squids from the Atlantic Ocean became available, the study was begun and soon grew with added material collected from the North Atlantic by various vessels of the U. S. Fish and Wildlife Service as well as those of the Institute of Marine Sciences. The study extended into Antarctic waters with the

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excellent growing collections of the USNS ELTANIN and was expanded to include the Pacific and Indian Oceans when material became available from various institutions on the west coast and elsewhere in the United States, as well as in Europe, Africa, Australia, and New Zealand.

In all, well over 600 specimens were studied, representing captures in every ocean except the Arctic. Though this is not a large number compared to that available in some groups, it is significant in this family, which is scarcely represented in most collections and where many of the species are known only by a few specimens.

In the course of this study a number of persons and institutions furnished information, loan of material and, in some cases, facilities for study; to them I wish to extend grateful thanks: Igor I. Akimushkin, formerly of the Institute of Oceanology, Academy of Sciences of the USSR; Gerald J. Bakus, Division of Marine Invertebrates, University of Southern California; Harvey R. Bullis, Jr., U. S. Fish and Wildlife Service, Pascagoula, Mississippi; William J. Clench, former Curator of Mollusks, and the late Richard W. Foster, Museum of Comparative Zoology, Harvard University; Jacques Yves Cousteau, Director, Institute of Oceanography, Monaco; R. K. Dell, Dominion Museum, Wellington, New Zealand; Ian Galbraith, formerly in charge of the mollusk collection, British Museum; J. R. Grindley and M. J. Penrith, South African Museum, Capetown; Fritz Haas, Curator of Lower Invertebrates, Chicago Natural History Museum; Willard D. Hartman, Curator of Invertebrates, Peabody Museum of Natural History, Yale University; Rudolf Kilias, Curator of Mollusks, Institut für Spezielle Zoologie und Zoologisches Museum, Humboldt Universität, Berlin; Jorgen Knudsen, Curator of Mollusks, Zoologiska Museum, Copenhagen; G. E. Maul, Curator, Museu Municipal de Funchal, Madeira; M. C. Mercer, Biological Station, Fisheries Research Board of Canada, St. John's, Newfoundland; Enrique Morales, Instituto de Investigaciones Pesqueras, Barcelona; Harald A. Rehder, Former Curator of Mollusks, U. S. National Museum; H. George Snyder, Scripps Institution of Oceanography, La Jolla; and the officials of the Musée d'Histoire Naturelle, Nice.

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HISTORICAL RÉSUMÉ

Férussac described the first species of histioteuthid squid in 1835 from a specimen taken alive in the Mediterranean by Verany. Férussac named it *Cranchia Bonnellii*. D'Orbigny in 1841 altered the specific name to *Bonelliana* (the spelling which has persisted almost exclusively to date), created a new genus for it, *Histioteuthis*, and placed it, along with the genera *Loligopsis* and *Chiroteuthis*, in the family Loligopsidae which he characterized as follows: "Point de sinus lacrymal. Tube locomoteur sans valvule et sans bride. Crête auriculaire nulle. Ouvertures aquifères anales nulles."

In 1849, Gray combined *Histioteuthis* and *Chiroteuthis* in his new family Chiroteuthidae. A new species was added to the genus in 1846 when Verany described *Ruppelli*. In his major work of 1851, Verany retained the classification proposed by d'Orbigny. In Steenstrup's (1861) reclassification of the oegopsids, *Histioteuthis*, along with *Chiroteuthis*, fell into his new family Taonoteuthi. Over the next few years the genus was generally referred to the Chiroteuthidae Gray except by Woodward (1871), who placed *Histioteuthis* in the family Teuthidae, subfamily Oegopsidae.

In 1879, Verrill described a new species, *Collinsii*, from an incomplete specimen taken off Nova Scotia and in the following year (1880a) described another new species from western North Atlantic waters, which he considered represented a new genus. He named it *Calliteuthis reversa*. Noting that the specimen had a siphon supported by a double dorsal bridle and possessed an internal valve, Verrill could not place it in *Histioteuthis* because of d'Orbigny's statement that members of the genus did not possess a funnel valve or bridle. Verrill therefore tentatively placed *Calliteuthis* in his family Mastigoteuthidae, stating that perhaps the genus might belong to the Chiroteuthidae. In the second part of this paper (1881a), Verrill erected the family Histioteuthidae to contain the lone genus *Histioteuthis*.

Hoyle (1885b) described a new squid, *Histiopsis atlantica*, about which he said: "evidently related both to *Histioteuthis* and to *Calliteuthis*, and in many respects is intermediate between them." In his report on the cephalopods collected by the CHALLENGER, Hoyle (1886) placed the three genera, together with *Chiroteuthis*, *Brachioteuthis*, and *Doratopsis*, into the family Taonoteuthi Steenstrup, subfamily Chiroteuthidae Gray. He noted d'Orbigny's erroneous description of *Histioteuthis* and since the characters of *Chiroteuthis* were still poorly understood, he combined all of these genera in his self-admittedly provisional classification.

Weiss (1889), after much study of the Chiroteuthidae during which he clarified the problem created by the erroneous characters attributed to the member genera by d'Orbigny, concluded that the family Taonoteuthi of Steenstrup should be abolished. He considered that the relationship of the group could best be shown by making the family Chiroteuthidae a sub-

family of the Ommastrephini along with Thysanoteuthidae, Ommastrephidae, and Mastigoteuthidae.

In 1896, when Goodrich described his new species *Histiopsis Hoylei*, he returned to the classification proposed by Hoyle (1886).

Joubin, in 1898, proposed a breakdown of the family Taonoteuthidae into two subfamilies on the basis of the presence or absence of luminous organs. Thus for the first time, the three genera *Histioteuthis*, *Histiopsis*, and *Calliteuthis* were united in the subfamily Histiototeuthinae.

Georg Pfeffer in 1900, gave the group full family status with the following diagnosis: "Zwei Reihen Näpfe auf den Armen, mehr als vier Reihen auf der Tentakelkeule, die sich bei den Erwachsenen nei in Haken verwandeln; Haftapparat eine Reihe von Näpfen und Knöpfchen, die sich über den Karpalteil und einen grossen Teil des Tentakelsteiles erstreckt." He included in the Histiototeuthidae two new genera, *Stigmatoteuthis* and *Meleagroteuthis*, erecting *Stigmatoteuthis* to contain Goodrich's species *Histiopsis Hoylei*, and *Meleagroteuthis* to contain a new species *hoylei*. Because of the lack of descriptions in this work, the latter species was a *nomen nudum* until he published a description of it in 1908.

Another significant decision of Pfeffer's contained in his 1900 "Synopsis der oegopsiden Cephalopoden" was the synonymizing of *Histioteuthis ruppelli* Verany, *H. collinsi* Verrill, and *Histiopsis atlantica* Hoyle with *Histioteuthis bonelliana*. By synonymizing *atlantica*, which has a seven-parted buccal membrane, with *bonelliana*, which has a six-parted membrane, Pfeffer gave rise to the concept that juveniles of *bonelliana* possess a seven-membered buccal membrane and adults a six-membered buccal membrane.

In his report on the collections of the PRINCESSE-ALICE, Joubin (1900) introduced into the subfamily Histiototeuthinae a new genus *Dubiototeuthis* containing his new species *physeteris*. Even though recognized almost immediately by other workers as belonging to the genus *Architeuthis*, *Dubiototeuthis* was still included in the Histiototeuthidae by Hoyle (1909) in his "Catalogue of Recent Cephalopoda."

Chun (1910) published the first comprehensive study of the family and gave detailed descriptions and illustrations of many structural parts. He considered the family to be comprised of two genera, *Calliteuthis* and *Histioteuthis* with the following diagnosis:

Arme frei, nur an der Basis durch Säume verbunden. Augen kegelförmig. Die hektokotylisierten Dorsalarms auf der Distalhälfte mit zweireihig angeordneten Saugnäpfen, die auf palisadenförmigen Stielen sitzen. Buccalhaut mit sieben Pfeilern. Männliche Leitungswege doppelt angelegt.
Calliteuthis

Arme, mit Ausnahme der Ventralarme und der Tentakel, durch ein Segel verbunden, welches aus verbreiterten Schutzsäumen hervorgeht. Augen Kugelig. Hektokotylisierte Dorsalarms auf der Distalhälfte mit vierreihig

angeordneten Saugnäpfen. Buccalhaut in der Jugend mit sieben, im Alter mit sechs Pfeilern. Männliche Leitungswege einfach angelegt.

Histioteuthis

Depending on the number of rows of photophores on the ventral arms, Chun divided *Calliteuthis* into two subgenera, *Stigmatoteuthis* containing *C. Hoylei* Goodrich, *C. ocellata* Owen, and *C. reversa* Verrill, and the subgenus *Meleagroteuthis* containing *C. meleagroteuthis* (Pfeffer) (= *Meleagroteuthis Hoylei* Pfeffer) and a new species *C. asteroessa*.

Pfeffer's (1912) major work "Die Cephalopoden der Plankton-Expedition" has been the most referred-to work in the modern history of the Histioteuthidae. He treated the family in considerable detail and considered it to be comprised of five genera, *Meleagroteuthis*, *Stigmatoteuthis*, *Calliteuthis*, *Histioteuthis*, and a new genus *Histiochromius*. *Stigmatoteuthis* was characterized as "Ringe der Arm- und Tentakelnäpfe gezähnt, Tentakelnäpfe ohne akzessorische Chitinbildungen," and *Calliteuthis* as "Ringe der Arm- und Tentakelnäpfe ungezähnt; Tentakelnäpfe mit akzessorischen Chitinbildungen." This distinction plagued workers for years, particularly the accessory chitinous structure, which Pfeffer never adequately described or illustrated. The type-species for the genus *Histiochromius* was based on a juvenile identified by Chun (1910) as a brachioeuthid, but, since it was obviously not a histioeuthid, the genus and species were never considered in future works on the family. Pfeffer compounded the confusion by adding to the family eight new species based mostly on juveniles or specimens inadequately described earlier by other workers and place by them in other families. Notable among these was *Loligo Meneghinii* Verany, 1851, which he made the type of *Calliteuthis Meneghini* and with which he synonymized Verrill's *Calliteuthis reversa*. Of Pfeffer's eight new species only one, *Stigmatoteuthis Dofleini* (= *Histioteuthis dofleini*), is considered valid in the present work. In general, cephalopod workers since Pfeffer have used his genera (except for *Histiochromius*), but usually with considerable dissatisfaction.

Over the next few years, three new species were added to the family, *Calliteuthis (Meleagroteuthis) heteropsis* Berry, 1913, *Meleagroteuthis separata* Sasaki, 1915, and *Calliteuthis miranda* Berry, 1918. During the years 1921-1925, interest was focused on the postembryological development of *H. bonelliana* and *C. reversa* (or *C. Meneghinii*) and several contributions were made by Grimpe, Naef, and Degner. Among other things, the concept that *bonelliana* has a seven-parted buccal membrane in the young and a six-parted one in the adult, as claimed by Pfeffer, was shown to be erroneous.

Robson, in his 1948 report on "The Cephalopoda Decapoda of the ARCTURUS Oceanographic Expedition, 1925," erected a new genus *Histiothauma* for a juvenile specimen, which he named *Histiothauma oceani*.

In the same paper, he described another new species of histioteuthid, *Stigmatoteuthis arcturi*.

Recent expeditions and collections have yielded additional records which have widened the known distribution of the histioteuthids and have produced several new species: *Histioteuthis cookiana* Dell, 1951, *Calliteuthis celetaria* G. Voss, 1960, *Calliteuthis celetaria pacifica* G. Voss, 1962, *Calliteuthis elongata* Voss & Voss, 1962, *Calliteuthis corona* Voss & Voss, 1962, and *C. inermis* Taki, 1964.

TAXONOMIC CONSIDERATIONS OF THE GENERAL MORPHOLOGY

The degree of variation or stability in the morphological characters of the histioteuthids has plagued workers since the description of the first species by Férussac in 1835.

In order to determine the taxonomic value of a character, it is necessary to know what changes are brought about during the growth of the individual, what is the amount, if any, of individual variation, and how the species varies over its geographical range. To accomplish this, it is desirable to study a large number of specimens covering a wide range in size and a wide geographical range. This was done as far as possible in the present work; well over 600 specimens were studied, ranging in size from about 3 to 185 mm ML and representing the thirteen valid species and two subspecies discussed in this paper. They were taken from every ocean except the Arctic.

The most striking character of the histioteuthids is the large number of *photophores* which cover the outer surface of the mantle, head, and arms, occurring in greatest concentration on the ventral surface. The individual photophore is a complex organ, and has been studied in detail by Joubin (1893) and Grimpe & Hoffman (1921). The photophores are set in diagonal rows throughout but, in conforming to the shape of particular parts of the body, they sometimes appear to be otherwise arranged as, for instance, a circlet around the eyelid margins and longitudinal rows on the arms. Photophores in this family have not been found on the funnel, fins, tentacles, eyes, or internally.

The colors display in life by the photophores have been described for *H. atlantica* as "bright spots of gold and cerise"; the enlarged photophores borne terminally on the arms were reported as "spots of luminous violet" (see p. 831, this paper). Verany (1851) described the photophores of *H. bonnellii* as being "opaline-yellow" in the posterior portion and "blue" in the anterior portion.

The details of the photophore pattern are of great taxonomic value. The particular pattern found in a species is remarkably constant even in animals found on both sides of an ocean or from one ocean to another. The number of longitudinal rows of photophores on the basal portion of arms IV is

of particular importance. In *meleagroteuthis* and *heteropsis*, there are about nine rows; in *miranda*, there are five rows; in *elongata*, *reversa*, and *corona berryi* there are four rows; and in the remaining six species or subspecies (the unique specimen of *bruuni* was denuded of skin, so its definitive photophore pattern is unknown), there are three longitudinal rows. The presence on the arms of an enlarged terminal photophore (*bonnellii*, *macrohista*), or series of enlarged photophores (*atlantica*), or a distinct terminal group of normal photophores (*celetaria celetaria*) is of specific importance.

The number of photophores forming the circlet around the margin of the right eyelid is significant (but not without an occasional exception). In *meleagroteuthis*, *heteropsis*, and possibly *bruuni*, there are usually 19-21 photophores; in *elongata*, *atlantica*, *reversa*, and *eltaninae* there are 18; in both subspecies of *celetaria* and of *corona*, in *dofleini* and *bonnellii*, there are 17; and in *macrohista* and *miranda* there are 16.

The photophores on the ventral surface of the mantle may all be of equal size, uniformly diminishing as the mantle narrows as, for example, in *dofleini*, or they may be of intermixed sizes as exemplified by *reversa*. The degree of concentration of the photophores varies from the dense crowding of small photophores found on *meleagroteuthis*, *heteropsis*, and possibly *bruuni*, to the less densely set pattern of slightly larger photophores found in *miranda*, to the more general pattern of larger photophores more widely set as in *dofleini*. In *elongata*, the large, dark, flat, oval photophores, lacking the typical large anterior lens, are unique. Some very large specimens of *bonnellii* have, in addition to the more observable described pattern of large photophores, a general scattering of minute photophores. These minute light organs may also be present in other species but only become apparent in the very large specimens.

The mantle is generally relatively short and conical in shape. In most of the species, the greatest mantle width, usually occurring just posterior to the anterior margin, is about 50 ± 10 per cent of the dorsal mantle length. In *bonnellii* and *macrohista*, the mantle is proportionately shorter and more broadly conical in shape, with a mantle width as much as 70-80 per cent of the mantle length; *H. elongata* on the other hand, has an unusually long slender mantle for a histioteuthid, with the mantle width being approximately 24-33 per cent of the mantle length. The mid anterodorsal margin of the mantle is typically produced into a low obtuse angle, the mid antero-ventral margin slightly excavated between the lateral angles. Distally, the mantle tapers to a blunt tip.

The skin, other than being beset with photophores, is not differentiated except in *dofleini*, in which it appears to be papillated, giving it a rough appearance. An important taxonomic character shared by *meleagroteuthis*, *miranda*, and *bruuni* is a row of small *tubercles* beneath the epithelium

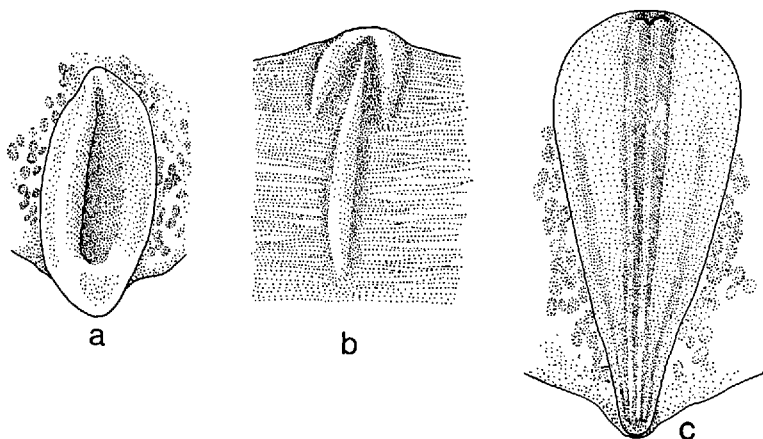


FIGURE 1. *Histioteuthis heteropsis* (Berry): a, left funnel cartilage; b, left mantle cartilage; c, dorsal cartilage.

along the midline of the anterior two-thirds of the dorsum of the mantle and the basal half of the dorsal three pairs of arms.

The *fins* are medium to large, ranging in length from about 30-60 per cent of the mantle length and in width from about 45 to over 90 per cent. The fin lobes are separate, free anteriorly but united posteriorly with a distinct median notch in the posterior margin. The posterior margin of the lobes may project as much as one-fourth of their length beyond the posterior tip of the mantle or they may terminate at the same level. The outline of the combined fins is transversely oval.

The small- to medium-sized *funnel* is supported from the head by a double bridle. The *funnel-mantle locking apparatus* is typical for the family. It consists of two rather long, slightly crescent-shaped, cartilaginous ridges lying parallel to the longitudinal axis of the mantle, one to either side on the ventrolateral surface of the inner mantle wall; each fits into a roughly oval funnel cartilage which is deeply excavated medially (Fig. 1, a, b).

A considerable degree of specific variation is displayed in the sculpture of the *funnel organ*. In general, the funnel organ may be described as an inverted V-shaped pad on the inner dorsal wall of the funnel and two oval or kidney-shaped pads, one on each side on the inner ventral wall of the funnel. The surface of the dorsal pad may be unsculptured as in *miranda*, *meleagroteuthis*, *heteropsis*, *bruuni*, and both subspecies of *celetaria*, or it may be permanently sculptured with a median ridge, developed to varying extents, extending down each arm, as in *atlantica*, *dofleini*, *macrohista*, *reversa*, and *eltaninae*. In *dofleini*, the posterior portion of the ridge is expanded into a distinct flap. In both subspecies of *corona*, the surface of the dorsal pad has the appearance of being distinctly swollen or of subse-

quent deflation. A well-developed semicircular *valve* is found in all species.

The *head* of a histioteuthid is large; in *bonnellii* and *macrohista*, its length may be in excess of 50 per cent of the dorsal mantle length; the head is usually as wide as, or slightly wider than, the mantle. The most conspicuous feature of the head is its asymmetry; the left eye is greatly enlarged (except perhaps in *elongata*), and may be twice the size of the right eye. To accommodate this disproportionate enlargement, the entire left side of the head is, as it were, stretched. The photophores thereon have the appearance of being less numerous and more widely spaced than on the right side. Further asymmetry is shown in *meleagroteuthis* and *miranda*, where the anterior end of the median row of tubercles on the left first arm makes a decided turn inward, a character not displayed on the corresponding right arm.

There is a *sinus* in the anteroventral margin of the eyelids in all species, though it may not always be conspicuous. One or two *nuchal folds* may be present but they are not conspicuous except in the two subspecies of *celetaria*. The *olfactory organ* is a simple fleshy papilla.

A study of the *buccal membrane* in the Histioteuthidae reveals important variations among the species. It is basically seven-parted, with seven lappets and seven supports, in all species except *bonnellii* and *bruuni*, in which it is six-parted. The method of attachment of the lappet supports to the arms falls into five basic patterns, diagrammed in Figure 2.

Patterns I and II are the commonest and are present in twelve members of the family. They differ only in the second support attachments which are bifurcate in I and single in II. In pattern III, found only in *macrohista*, the fourth supports each have an extra attachment to the junction of the web between the third and fourth arms on the respective sides. In pattern IV, which occurs only in *bonnellii*, a single fourth lappet and support with multiple attachments replaces the more common two fourth members. *H. bruuni* has a unique asymmetrical pattern (V); here a single lappet and support with a bifurcate attachment replaces the usual left third and fourth members. The attachments of the second supports display additional asymmetry; the second support attachment is bifurcate on the right side, while it is single on the opposite side. Each species has a consistent pattern, except for *meleagroteuthis* and *heteropsis*, which display both patterns I and II, and sometimes have the attachments of the second supports bifurcate on one side and single on the other.

The development of the *inner web*, connecting the inner margins of the arms, varies in the family from vestigial to low, as in *elongata*, *dofleini*, *reversa*, *eltaninae*, and both subspecies of *celetaria*; to moderate (approximately 10-30 per cent of the length of the longest arm), as in *atlantica*, *miranda*, *meleagroteuthis*, both subspecies of *corona*, and possibly *bruuni*; to deep (in excess of 50 per cent of the length of the longest arm) as found

Buccal Membrane Patterns

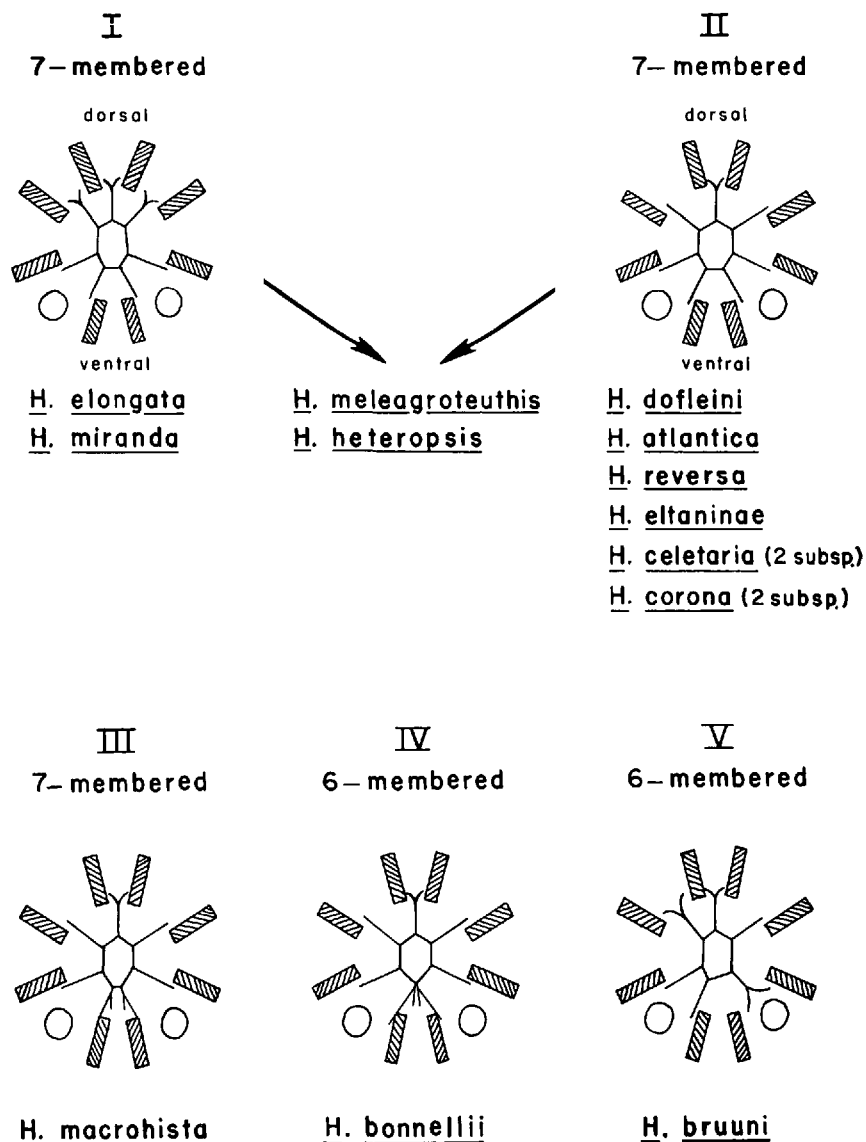


FIGURE 2. Buccal membrane patterns occurring in the Histioteuthidae.

in *bonnellii*, and *macrohista*. Only in *dofleini* is the *outer web*, rather than the inner web, developed to any extent.

The arms are long and, except in *elongata*, they may be two or three times longer than the mantle. Usually arms II and III are nearly coequal and are the longest; arms I and IV are either nearly coequal or I may be slightly longer than IV. The typical arm formula for the family is either $2 = 3.1 = 4$ or $2 = 3.1.4$. The arms are stout basally and taper to delicate tips. The distal two-thirds to one-half of arms I and II bear a low median *keel* on their aboral surface. On arms III, the keel usually originates near the base of the arm, with the central portion moderately expanded into a *swimming keel*.

On the oral surface, the arms bear two rows of small- to moderate-sized *suckers*. The suckers on arms I, II, and III are roughly coequal in size, or largest on the third quarter of the arm. On arms IV, the suckers are usually one-third to one-half the size of those on the other arms.

In the Histioteuthidae too much importance as a sole taxonomic character has been placed on the presence or absence of teeth on the horny rings of the arm suckers. Pfeffer (1912) used the presence or absence of teeth as a generic difference between *Calliteuthis* and his *Stigmatoteuthis*. Though a specific pattern of dentition or lack of it appears to be typical for a species, it is not always consistent. Teeth, when present, are usually low, broad, and round or square, and, on the greater extent of the arm, confined generally to the distal margin of the rings; the proximal margin is usually smooth or irregular. The small suckers on the distal quarter of the arm and suckers on arms IV often have a greater number of teeth than the other arm suckers.

In the species *eltaninae*, *dofleini*, *bonnellii*, *macrohista*, *miranda*, *melagroteuthis*, *heteropsis*, and *bruuni*, the rings are toothed, the number varying from as few as 4-10, common in *bonnellii* and *macrohista*, to as many as 28 in *dofleini*. The suckers on the major portion of arms I-III are typically smooth in *elongata*, *celetaria*, and *corona*, but the suckers on arms IV and on the tips of the other arms are usually armed with small teeth. The sucker rings on arms I-III in *atlantica* vary from almost smooth to being incised with 5-10 teeth. The rings in *reversa* may or may not be incised.

Where *hectocotylization* was noted in seven species, the distal portion of both first arms was affected. The pedestals of the suckers were enlarged and closely set marginally, giving a palisading effect on side view, and leaving a distinct central channel between the two rows. Chun (1910) described the hectocotylus of *H. Rüppelli* (= *H. bonnellii*) as having four rows of suckers. I was not able to definitely confirm this, as only juveniles of this species have been at my disposal during the major part of this study. In some, the suckers do appear to be in four rows, while in others they appear to lie in two.

The basal portion of the *protective membranes* is developed in some species into the inner web, described earlier. At the distal termination of the web, the protective membranes continue up the arm, low and marginal. Only in *dofleini* are they conspicuously trabeculate.

The *tentacles* are long, up to almost four times the mantle length, and each ends in an expanded *club*. The manus of the club is relatively broad and the dactylus attenuate, both being about coequal in length. There is a low median *swimming keel* on the distal half of the aboral surface of the club; on the proximal half, a deep longitudinal *cleft* is often present in *reversa*, *dofleini*, and *atlantica*.

On the oral surface, the *carpal adhesive apparatus* extends down the ventral margin of the tentacular stalk for a distance of approximately one to three times the club length. The arrangement of the suckers and pads is specific, but occasionally a sucker or pad will be missing. The arrangement on one tentacle has its mirror image (i.e., suckers in position of pads, and vice versa) on the other, but it is not always consistent in a species as to which tentacle has which arrangement, and occasionally as found in the study of *corona corona*, a combination of the two arrangements will be present. Often the sucker (or corresponding pad) lying at the base of the manus is enlarged; in *atlantica* this sucker may also have a conspicuous accessory growth on one side of the ring.

The suckers on the manus are set in five to eight longitudinal rows; often, as in *reversa*, *eltaninae*, and *atlantica*, several of the centralmost ones are enlarged, sometimes as much as three to four times the size of the other suckers. The horny rings are usually incised with pointed triangular or long slender straight-sided blunt teeth around their entire margin except in *celetaria celetaria*, in which only the distal margin bears teeth. The exact number of teeth is not specific but a definite range seems to be typical for a species; for instance, in *celetaria celetaria*, the number of teeth on the central suckers of the manus is usually 12-14, in *corona corona* 33-55, and in *dofleini* 50-70. The teeth on these large suckers are often either shorter and heavier on the proximal margin than on the distal margin, or small and numerous on the proximal margin and large and widely set on the distal margin.

Certain species exhibit unique characters in regard to certain suckers on the manus. In *atlantica*, the much enlarged central suckers are very irregularly incised, with the margin of a single sucker ranging from smooth, to irregular, to distinctly toothed. In adult *dofleini*, the sucker rings of the ventral submedian row have an accessory growth of a series of teeth or nobs projecting out from the dorsal side of the base of the ring. In both subspecies of *celetaria*, the proximal suckers of the ventral rows have distinct asymmetrical denticulate collars with the ventral portion abnormally broadened, thereby giving these suckers a roughly triangular appearance.

On the dactylus, the closely set suckers are uniformly small and regularly decrease in number as the club narrows. Along either margin of the manus there is a low protective membrane which all but disappears on the dactylus.

A comparative study of the internal anatomy remains to be done for the histioteuthids. In regard to the male *genitalia*, *dofleini* is unique in the family in possessing a double set of functional organs, one to either side, while the remaining species have a single set on the left side. The female *genitalia* appears normal, accompanied by two nidamental glands in all species.

Mature *spermatophores* were obtained from nine species (Figs. 3, 4). They are distinct for each species and display varying degrees of individual and possibly geographic variation. Within a single lot from the same specimen, the spermatophores are identical except for some proportional differences (sometimes as high as 20 per cent) in the size of the three composite parts—ejaculatory apparatus, cement body, and sperm mass. Variation within a species which might be attributed to geographic isolation was found in two species, *reversa* and *dofleini*. In *reversa*, this variation is a distinct proportional one, while in *dofleini* it is structural. A character shared by all species, except *dofleini* from the Gulf of Mexico (spermatophores available from only a single specimen), is a single large loop in the ejaculatory apparatus. All but three of the species, *dofleini*, *eltaninae*, and *atlantica*, have a connective complex between the cement body and the ejaculatory apparatus consisting of an outer collar, or collars, intervening cavity or cavities, and a central pedestal which gives rise to the ejaculatory tube, with each species displaying its own specific modifications. The proportional lengths of the three composite parts show great variation from species to species, i.e., the sperm mass varies in length from 3 to 8 per cent of the length of the spermatophore in *eltaninae*, *atlantica*, and *macrohista*, to 34 to 43 per cent in *reversa*, *bruuni*, and *dofleini*.

Several characters may be considered to be typical of the *beaks* or *mandibles* of the histioteuthids (Figs. 5, 6). The upper beak has a moderately long curved rostrum that usually has an obtuse or false jaw angle. The lower beak has an obtuse jaw angle and usually a median ridge bisecting the lateral wall from the midanterior margin to the midposterior point.

A comparison of the *radulas* (Figs. 7, 8) shows a general similarity of all the teeth except for the third laterals which are typically long and saber shaped. There is a tendency for the first and second laterals to be very similar to the rhachidian in both size and shape rather than to be asymmetrical. The occurrence of marginal plates is irregular, and when present, they are often poorly developed. The radulas of the species examined show the two extremes of types. In *atlantica*, the teeth approach a general homodont condition, while in *bonnellii* and *corona corona* the teeth are definitely heterodont. The other species range between these forms.



FIGURE 3. Spermatophores: a-b, *Histioteuthis dofleini* (Pfeffer), O 3733; c, *H. dofleini*, redrawn from Sasaki (1929); d-e, *H. eltaninae*, n. sp., holotype; f-g, *H. reversa* (Verrill), specimen from off Blanes, Spain; h, *H. reversa*, Del 62-11; i-j, *H. bruuni*, n. sp., holotype; k, *H. atlantica* (Hoyle), D 3975 VI.

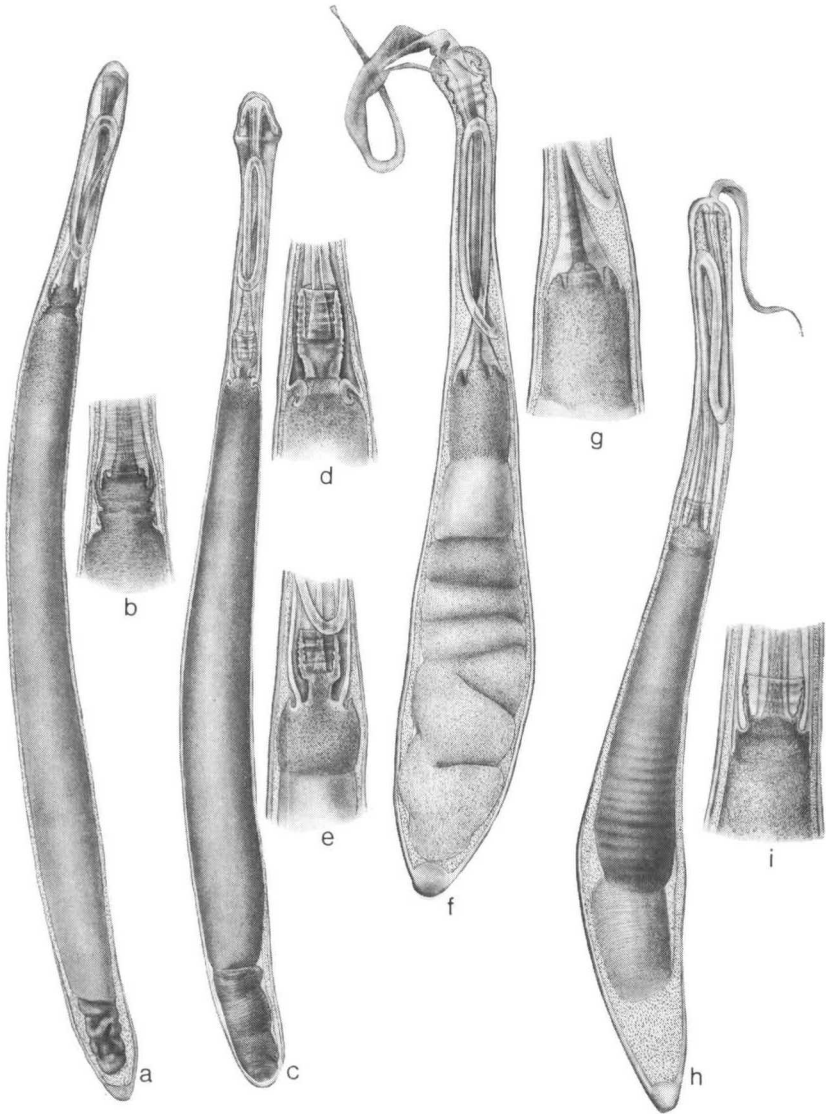


FIGURE 4. Spermatoophores: a-b, *Histioteuthis macrohista*, n. sp., SS PICKLE 542; c-d, *H. heteropsis* (Berry), AHF 8291; e, *H. heteropsis*, AHF D5693; f-g, *H. corona corona* (Voss & Voss), O 4300; h-i, *H. celetaria pacifica* (G. Voss), paratype, Alb D5221.

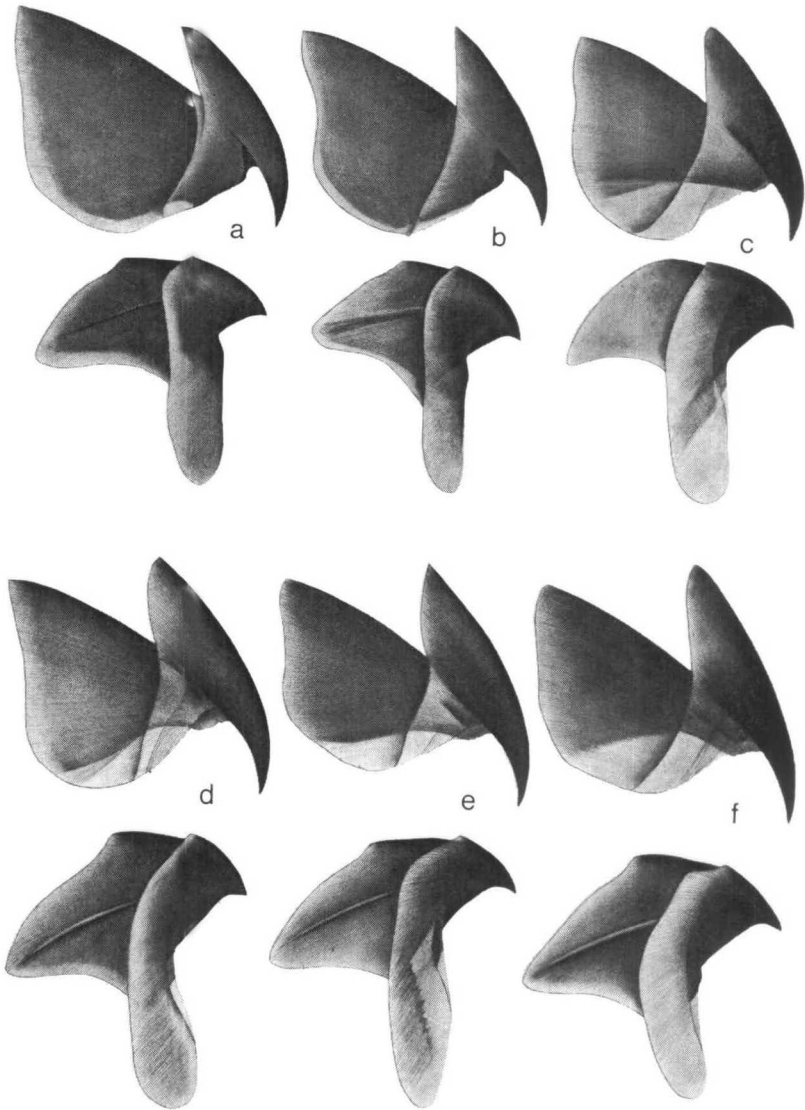


FIGURE 5. Mandibles: a, *Histioteuthis elongata* (Voss & Voss), paratype, YPM 12440; b, *H. reversa* (Verrill), specimen from off Blanes, Spain; c, *H. eltaninae*, n. sp., paratype, USNM 576170; d, *H. celetaria pacifica* (G. Voss), G 202; e, *H. dofleini* (Pfeffer), UMML 31.385; f, *H. dofleini*, Elt 1803.

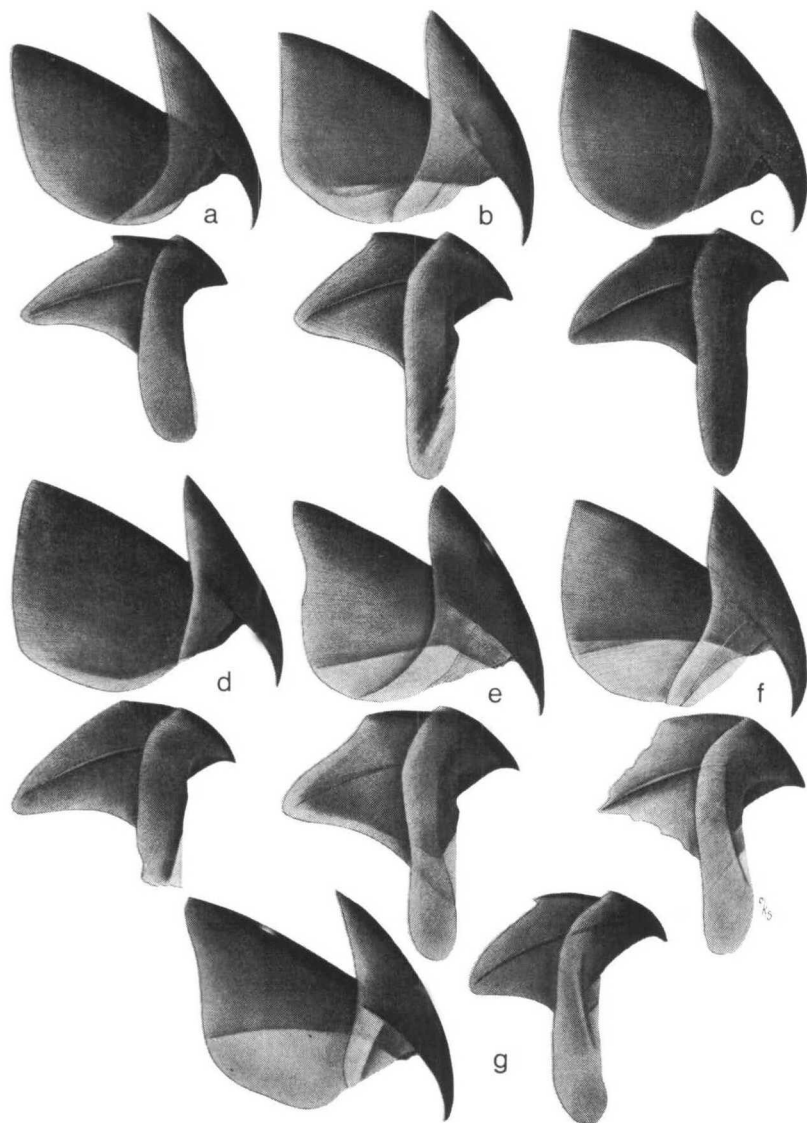


FIGURE 6. Mandibles: a, *Histioteuthis corona corona* (Voss & Voss), O 3653; b, *H. meleagroteuthis* (Chun), D 1163 II; c, *H. bruuni*, n. sp., holotype; d, *H. heteropsis* (Berry), AHF D5693; e, *H. atlantica* (Hoyle), DMNZ-M9830; f, *H. macrohista*, n. sp., paratype, USNM 576176; g, *H. bonnellii* (Férussac), redrawn from Naef (1921).

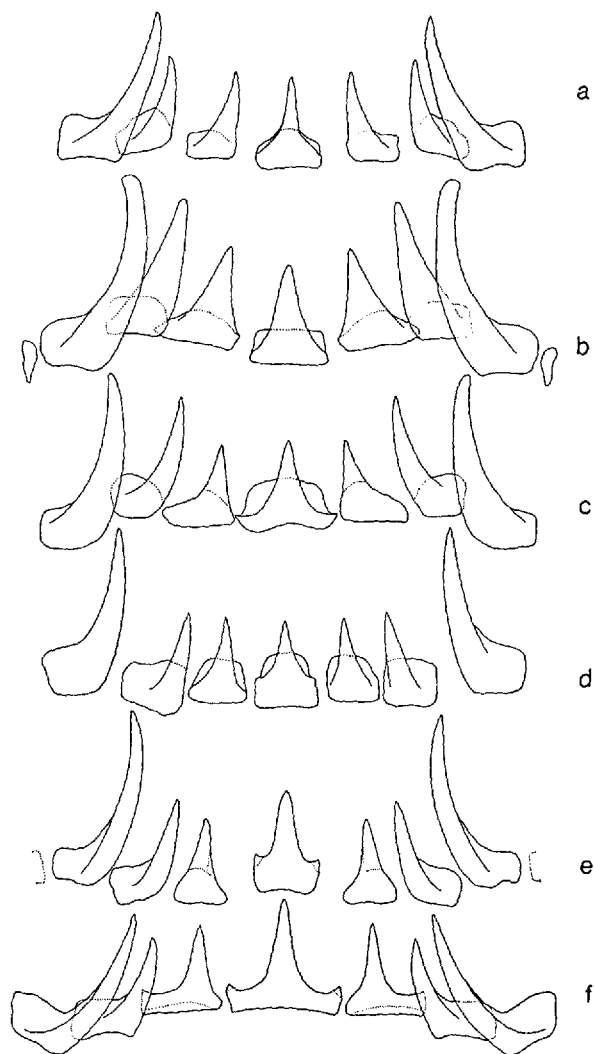


FIGURE 7. Radulas: a, *Histioteuthis elongata* (Voss & Voss), USNM 78083; b-c, *H. reversa*, specimens from off Blanes, Spain; d, *H. eltaninae*, n. sp., paratype, Elt 354-20; e, *H. celetaria pacifica* (G. Voss), G 202; f, *H. corona corona* (Voss & Voss), O 3653.

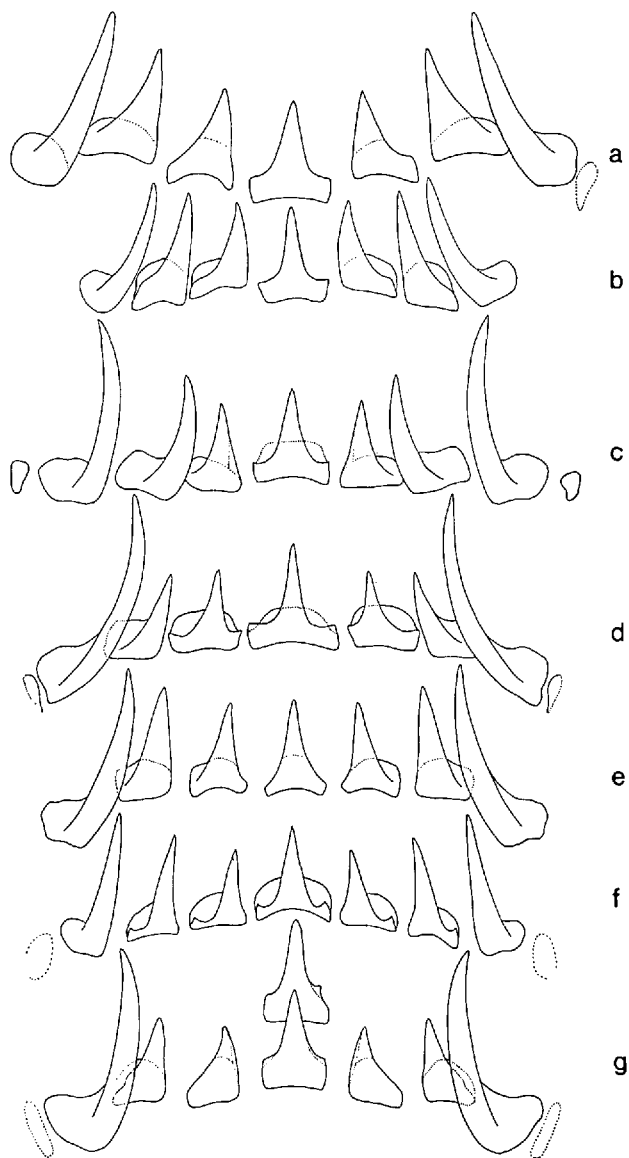


FIGURE 8. Radulas: a, *Histioteuthis dofleini* (Pfeffer), *Elt* 1803; b, *H. dofleini*, specimen from off Miami; c, *H. meleagroteuthis* (Chun), *D* 1342 VIII; d, *H. heteropsis* (Berry), AHF D5693; e, *H. atlantica* (Hoyle), DMNZ M9830; f, *H. bonnellii* (Férussac), redrawn from Naef (1921); g, *H. macrohista*, n. sp., paratype, USNM 576176.

The delicate, translucent, lightly pigmented *gladius* typical of the family is deeply concave on its ventral surface, with a long, moderately broad vane that ranges in length from about 65 to 84 per cent of the total length of the *gladius* and in width from about 18 to 30 per cent of the total length of the *gladius*. The *gladius* tapers posteriorly to a blunt end, with the margins of the vane and the distal tip of the *rhachis* curled inward.

GROWTH

In the histioteuthids, growth is accompanied by varying proportional changes in the animal and introduces and accentuates certain characters. In general, with increased total size, the arms become proportionately longer, the mantle proportionately narrower, the fins proportionately smaller, and the web, if developed in a species, becomes deeper.

The suckers on the manus of the tentacular club usually undergo considerable change with increased size of the animal. The median suckers may become disproportionately large, depending on the species, and in general the dentition tends to become more irregular. In *dofleini*, an accessory growth of teeth or knoblike projections from the base of the rings of the suckers of the ventral submedian row is present in adults but is not found in the small juveniles. In *celetaria celetaria*, and probably *c. pacifica*, the asymmetrical development of the denticulate collar of certain suckers of the manus is not apparent in juveniles of 10 mm ML, but apparently develops gradually as the animal grows.

In *meleagroteuthis*, the characteristic median row of tubercles on the dorsal arms and the mantle do not make their appearance until the juvenile is about 14 mm ML; thereafter, the tubercles increase in number as the animal grows. This is probably also the case in *miranda* and *bruuni*.

The general pattern of photophores for a species is apparent in juveniles below 10 mm ML, but as the animal grows, the number of photophores comprising the pattern may increase. The final number making up a particular pattern may be established earlier in one pattern than in another. For instance, the adult number of photophores in the circlet around the right eyelid is present in young as small as 8 mm ML, while the number of enlarged photophores making up the unique terminal group on the dorsal three pairs of arms in *atlantica* increases as the animal grows. In *bonnellii* and *macrohista*, the characteristic, single, enlarged terminal photophore on the dorsal arms can be seen in young of 7-8 mm ML, and it becomes disproportionately larger with the growth of the individual.

Indications of the definitive sculpture of the dorsal pad of the funnel organ, which is characteristic of some species, may be apparent in the very young (at about 7 mm ML in *dofleini*) and is accentuated by growth of the individual.

The beaks undergo obvious changes with growth of the individual; they

become increasingly more chitinized and pigmented and the hook of the rostrum becomes more accentuated.

FOOD

An extensive study was not done, but the stomachs of a number of specimens of different species were opened for food analysis. No intact organisms were found, but there were recognizable remains of fish (scales, bones, otoliths), crustaceans (pieces of exoskeleton), and squid (beaks), in that order of predominance.

GENERAL DISTRIBUTION

The histioteuthid squids obviously occur in large numbers, as shown by stomach analysis of sperm whales and certain predatory fishes and oceanic birds, which prove to be much more efficient in capturing these elusive animals than even our largest nets.

All of the species occupy a broad vertical range of distribution which transcends zonal boundaries. The family may be described as primarily mesopelagic but with most members frequenting either the epipelagic zone above or the bathypelagic zone below, or both zones. *H. dofleini*, *bonnellii*, and *meleagroteuthis* appear to be most common in depths of about 100 to 700 or 800 meters and are only occasionally taken deeper. On the other hand, *eltaninae*, *macrohista*, and *atlantica* are regularly found in the deeper waters at 2000 meters or more and are only rarely captured in the upper 200 meters. Regardless of latitude, if the species is present, it seems to occupy the same vertical zone.

Though only one species, *heteropsis*, is definitely known to migrate vertically diurnally (Young, in manuscript), it is very possibly a characteristic of most, if not all, of the species of the family.

There are no indications of a depth preference for the different growth stages, for both adults and small juveniles of all the species have been found throughout the depth range.

Though a considerable range of temperature is necessarily tolerated in living over such a broad range of depth, temperatures in the preferred vertical column appear to play an important role in governing the geographic distribution of a species. A preference for the lower temperatures appears to limit *eltaninae*, *atlantica*, and *macrohista* primarily to the subantarctic region, with *eltaninae* possibly exhibiting the narrowest tolerance and hence the more restricted geographic distribution. A preference for the higher temperatures is shown by the records for captures of *dofleini* in the Atlantic, where all specimens have been taken between latitudes of 15° and 36° N. This same species is exceptionally euryhaline. It has been taken in considerable numbers in the Gulf of Mexico at the mouth of the Mississippi, as well as in the Sargasso Sea.

Such widespread species as *reversa* and *meleagroteuthis* appear to prefer the more moderate temperatures. There are good indications that in at least three species, *reversa*, *dofleini*, and *corona*, subspecific segregation has occurred and we are dealing with two or more separate breeding populations, which very probably have different physiological tolerances.

A definite relationship exists between the regions of moderate to high organic productivity in the oceans and the geographic distribution of the histioteuthids. With the exception of *dofleini* in the Atlantic, all of the species are found in waters underlying areas of moderate to high organic productivity.

These considerations on distribution of the histioteuthids are necessarily and intentionally general, for our knowledge of this group of squids is still fragmentary at best.

The species known to occur in the major oceanic areas are as follows:

NORTH ATLANTIC	SOUTH ATLANTIC
<i>H. elongata</i>	<i>H. reversa</i>
<i>reversa</i>	<i>c. corona</i>
<i>c. celetaria</i>	<i>atlantica</i>
<i>dofleini</i>	<i>bonnellii</i>
<i>c. corona</i>	<i>macrohista</i>
<i>bonnellii</i>	<i>meleagroteuthis</i>
<i>meleagroteuthis</i>	<i>bruuni</i>
NORTH PACIFIC	SOUTH PACIFIC
<i>H. celetaria pacifica</i>	<i>H. atlantica</i>
<i>corona berryi</i>	<i>macrohista</i>
<i>dofleini</i>	<i>miranda</i>
<i>miranda</i>	<i>meleagroteuthis</i>
<i>meleagroteuthis</i>	<i>heteropsis</i>
<i>heteropsis</i>	<i>dofleini</i>
INDIAN OCEAN	ANTARCTIC
<i>H. celetaria pacifica</i>	(SUBANTARCTIC REGION)
<i>dofleini</i>	<i>H. eltaninae</i>
<i>c. corona</i>	<i>atlantica</i>
<i>atlantica</i>	<i>macrohista</i>
<i>bonnellii</i>	<i>miranda</i>
<i>meleagroteuthis</i>	
<i>macrohista</i>	

The charts of geographic distribution given for each species are intended to give the general picture of known world distribution. In cases where a large number of records occur in close proximity, a single location symbol may represent more than a single record for the sake of clarity in presentation. Exact data may be found in the text. Because of the confusion of characters and hence species in the past, only those records of specimens which could be definitely identified either through examining the material or through the text itself were included in the charts and synonymies.

MEASUREMENTS, INDICES, AND ABBREVIATIONS

All terms, measurements (in mm), and derived indices are as defined by G. Voss (1963), with the few following exceptions. The spermatophores are studied in added detail, using the general terminology of Drew (1919) (Fig. 9). The following measurements and indices for spermatophores are used:

SpL, spermatophore length: total length of spermatophore.

SpLI, spermatophore length index: total length of spermatophore as a percentage of mantle length.

SpWI, spermatophore width index: width of spermatophore as a percentage of spermatophore length.

SpMI, sperm mass index: length of sperm mass as a percentage of spermatophore length.

CBI, cement body index: length of cement body as a percentage of spermatophore length.

EjAI, ejaculatory apparatus index: length of ejaculatory apparatus as a percentage of spermatophore length.

Two additional indices introduced in the study of the gladius are:

GVLI, gladius vane length index: length of vane as a percentage of gladius length.

GVWI, gladius vane width index: greatest width of vane as a percentage of gladius length (=GWI of G. Voss [1963]).

In the study of *H. dofleini*, the index for the outer web (OWI) was used rather than that for the inner web (IWI) used in the other species.

A great deal of shrinkage occurs in these squids as a result of preservation. Specimens in buffered formalin appear to suffer less than those in alcohol. In *H. elongata*, some individuals have undergone as much as 20 to 30 per cent shrinkage, and as a result, the gladius is much folded upon itself inside the specimen. Thus in this species, gladius length (GL) is substituted for mantle length. Mantle length (ML) in all cases refers to the dorsal length of the mantle.

In the descriptions of the carpal adhesive apparatus, the abbreviation "p" is used for pad, and "s" for sucker.

The following abbreviations for the source or deposition of the material are used:

AHF—Allan Hancock Foundation, University of Southern California.

AM—Australian Museum, Sydney.

AUZ—Zoology, Auckland University, New Zealand.

BANZARE—British, Australian, New Zealand Antarctic Research Expedition.

BM(NH)—British Museum, Natural History.

CNHM—Chicago Natural History Museum.

DMNZ—Dominion Museum, Wellington, New Zealand.

IOM—Musée Océanographique, Monaco.

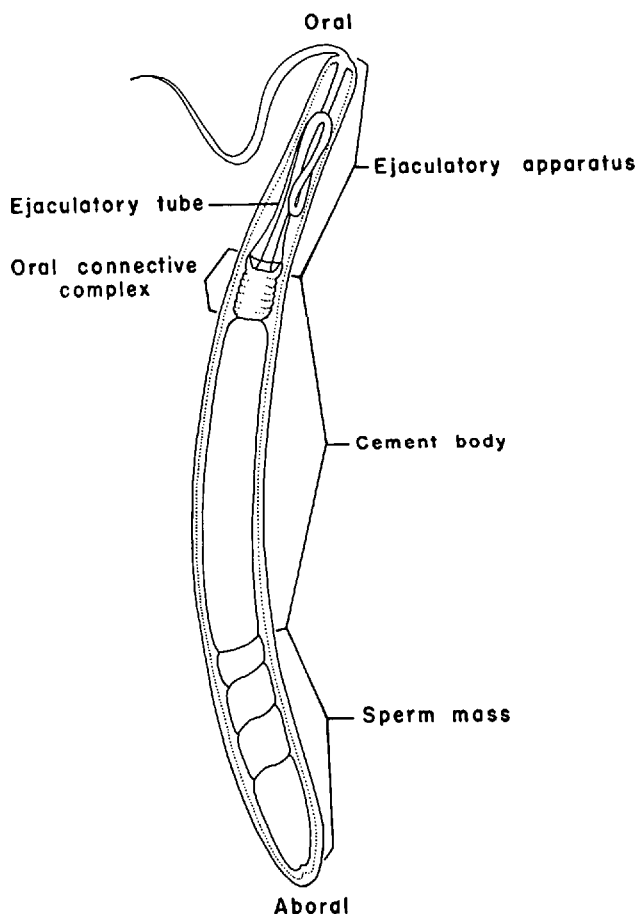


FIGURE 9. Details of spermatophore.

MCZ—Museum of Comparative Zoology, Harvard.
MHNN—Musée d'Histoire Naturelle, Nice.
MMF—Museu Municipal de Funchal, Madeira.
SAM—South African Museum, Capetown.
SIO—Scripps Institution of Oceanography, California.
UMML—University of Miami, Marine Invertebrate Museum.
USNM—United States National Museum.
UW—University of Washington.
YPM—Peabody Museum, Yale University.
ZMUC—Zoologisk Museum, København.

In addition, the following abbreviations for collecting vessels appear in the tables of data and the captions for figures:

AB—U.S. R/V ANTON BRUUN

Alb—U.S. Fisheries steamer ALBATROSS

Atl—Woods Hole Oceanographic R/V ATLANTIS

Chal—HMS CHALLENGER

D—Danish research ship DANA

Del—U.S. Fish and Wildlife M/V DELAWARE

Elt—USNS ELTANIN

G—Danish research ship GALATHEA

O—U.S. Fish and Wildlife M/V OREGON

SB—U.S. Fish and Wildlife M/V SILVER BAY

V—Allan Hancock Foundation R/V VELERO IV

Collecting depths for specimens collected by the DANA and GALATHEA are given in meters of wire (mw). The abbreviation "IKMT" indicates the Isaacs-Kidd midwater trawl.

KEY TO THE SPECIES OF THE FAMILY HISTIOTEUTHIDAE

1. Median ridge of tubercles on dorsal surface of mantle and basally on arms I, II, and III (Specimens over about 16 mm ML) 2
 No median ridge of tubercles on dorsal surface of mantle and basally on arms 4
2. Buccal membrane six-membered *H. bruuni*, n. sp.
 Buccal membrane seven-membered 3
3. Photophores on ventral surface of mantle and head uniformly small, densely set; approximately 24-27 photophores in diagonal row originating at lateral angle on ventral surface of mantle; in 8-9 longitudinal rows on arms IV; 19-21 photophores in circlet around margin of right eyelid *H. meleagroteuthis* (Chun, 1910)
 Photophores on ventral surface of mantle and head less densely set; approximately 12 photophores in diagonal row originating at lateral angle on ventral surface of mantle; in 5 longitudinal rows on arms IV; 16 photophores in circlet around margin of right eyelid *H. miranda* (Berry, 1918)
4. Single enlarged, elongate photophore present terminally on arms I, II, and III; inner web deep, in excess of 50 per cent of length of longest arm 5
 Single enlarged, elongate photophore not present terminally on arms I, II, and III; inner web vestigial to moderate in depth, less than 50 per cent of length of longest arm 6
5. Buccal membrane six-membered; 17 large photophores in circlet around margin of right eyelid *H. bonnellii* (Férussac, 1835)
 Buccal membrane seven-membered; 16 large photophores in circlet around margin of right eyelid *H. macrohista*, n. sp.

6. Photophores on ventral surface of mantle and head small, densely set; approximately 19-22 photophores in diagonal row originating at lateral angle on ventral surface of mantle; in 8-9 longitudinal rows on arms IV; 19-21 photophores in circlet around margin of right eyelid *H. heteropsis* (Berry, 1913)
 Photophores on ventral surface of mantle and head mostly large, less densely set; usually approximately 9-10 photophores in diagonal row originating at lateral angle on ventral surface of mantle; in 3-4 longitudinal rows on arms IV; 17-18 photophores in circlet around margin of right eyelid 7
7. Distinct terminal group of photophores present on arms 8
 No distinct terminal group of photophores present on arms 9
8. Series of several enlarged photophores present terminally on arms I, II, and III; inner web moderately developed to depth of about 17-30 per cent of length of longest arm; dorsal pad of funnel organ sculptured with median ridge down each arm; strong nuchal folds not apparent; no unusual development of denticulate collar of suckers on manus of club *H. atlantica* (Hoyle, 1885)
 Terminal group of several normal-sized photophores separated by a distinct space present on all four pairs of arms; inner web vestigial; dorsal pad of funnel organ unsculptured; 2 strong nuchal folds present; suckers along ventral margin of manus of club with denticulate collar broadened into plate
 *H. celetaria celetaria* (G. Voss, 1960)
9. Mantle elongate; large atypical round or oval black photophores present on posterior third of ventral surface of mantle and distal portion of arms *H. elongata* (Voss & Voss, 1962)
 Mantle conical; large atypical photophores not present 10
10. Dorsal pad of funnel organ sculptured with median ridge down each arm; horny rings of arm suckers usually toothed 11
 Dorsal pad of funnel organ unsculptured, surface may have swollen or deflated appearance; horny rings of majority of suckers on arms I, II, and III usually smooth 13
11. Distal portion of median ridge on arms of dorsal pad of funnel organ expanded into distinct flap; outer web conspicuously developed up to depth of 14 per cent of length of longest arm; genitalia double in male; 17 large photophores in circlet around margin of right eyelid *H. dofleini* (Pfeffer, 1912)
 Distal portion of median ridge on arms of dorsal pad of funnel organ not expanded into flap; outer web not conspicuously developed; genitalia in male single; 17 large and 1 small photophore in circlet around margin of right eyelid 12
12. Arms IV with 4 longitudinal rows of photophores, 3 rows of

large organs (dorsalmost row of large photophores with five to eight organs) and 1 dorsal marginal row of small organs

..... *H. reversa* (Verrill, 1880)

Arms IV with 3 longitudinal rows of photophores, 3 rows of large organs (dorsalmost row of large photophores with 2 to 3 organs), no dorsal marginal row of small organs *H. eltaninae* n. sp.

13. Arms IV with 4 longitudinal rows of photophores, all large

..... *H. corona berryi* n. subsp.

Arms IV with 3 longitudinal rows of photophores, all large

..... *H. corona corona* (Voss & Voss, 1962)

The only known valid species of histioteuthid not contained in this key is *H. celetaria pacifica* (G. Voss, 1962). The skin on the arms of all the specimens available has been in such poor condition that the exact photophore pattern thereon is not known, thereby making their position in the key uncertain. Since the status of Taki's species *inermis* is uncertain (see p. 852, this paper), it, too, was excluded from the key.

Order TEUTHOIDEA

Suborder OEGOPSIDA

Family HISTIOTEUTHIDAE Verrill, 1881

Loligopsidae (in part), d'Orbigny, 1841: xxxvii.—Verany, 1851: xi.

Chiroteuthidae (in part), Gray, 1849: 42.—Tryon, 1879: 165.—Fischer, 1887: 340.

Taonoteuthi (in part), Steenstrup, 1861: 69.—Jatta, 1896: 107.

Cheiroteuthidae (in part), Keferstein, 1865: 1445.

Teuthidae, Subf. Oegopsidae (in part), Woodward, 1871: 170.

Mastigoteuthidae (in part), Verrill, 1881b: 117.

Histioteuthidae Verrill, 1881a: 431.—Pfeffer, 1900: 168.—Chun, 1910: 147.

—Naef, 1923: 343.—Joubin, 1924: 61.—Dell, 1959: 98.

Taonoteuthi, Subf. Chiroteuthidae (in part), Hoyle, 1886: 42.

Ommastrephini, Subf. Chiroteuthidae (in part), Weiss, 1889: 93.

Taonoteuthi, Subf. Cheiroteuthidae (in part), Goodrich, 1896: 15.

Taonoteuthidae, Subf. Histioteuthinae, Joubin, 1898: 112.

Taonoteuthi, Subf. Histioteuthidae, Fischer & Joubin, 1906: 341.

Taonoteuthidae, Subf. Histioteuthinae (in part), Joubin, 1900: 96.

Histioteuthidae (in part), Hoyle, 1909: 271.—Pfeffer, 1912: 241.

Medium to large squid; mantle usually short and conical (except in *elongata*); head large with asymmetrically developed eyes, left eye usually much the larger; fins medium to large, transversely oval in combined outline, united posteriorly with median notch; fins may extend slightly posterior to free tip of mantle; numerous small photophores set irregularly in diagonal rows on skin of mantle, head and aboral surface of arms, more concentrated on ventral surface; inner web connecting arms vestigial to in excess of 60 per cent of length of arms; six- or seven-parted buccal membrane; suckers unmodified in two rows on arms and usually 5-8 rows on tentacular club;

tentacles long, carpal adhesive apparatus extends two to three club lengths down oral surface of stalk; both arms I usually hectocotylyzed in male; male genitalia single (except in *dofleini*).

Type-genus.—*Histioteuthis* d'Orbigny, 1841.

Genus *Histioteuthis* d'Orbigny, 1841

Cranchia (in part), Férussac, 1835.

Histioteuthis d'Orbigny, 1841: xxxvii; 1848: 327.—Chun, 1910: 147.—Pfeffer, 1912: 297.—Naef, 1923: 362.—Dell, 1959: 98.

Calliteuthis Verrill, 1880: 393.—Chun, 1910: 149.—Pfeffer, 1912: 250.—Naef, 1923: 352.—Dell, 1959: 99.—Voss & Voss, 1962: 169.

Loligopsis (in part), Owen, 1881: 139.

Histiopsis Hoyle, 1885b: 201; 1886: 180.—Goodrich, 1896: 15.—Pfeffer, 1900: 170.—Dell, 1959: 98.

Meleagroteuthis Pfeffer, 1900: 170; 1912: 290.—Chun, 1910: 170.—Sasaki, 1929: 262.—Dell, 1959: 99.

Stigmatoteuthis Pfeffer, 1900: 170; 1912: 279.—Sasaki, 1929: 258.—Akimushkin, 1963: 193.

Histiotauma Robson, 1948: 123.—Dell, 1959: 98.

Since the family is monotypic, the generic diagnosis is the same as that of the family.

Type-species.—*Histioteuthis Bonelliana* Férussac, 1835 (= *Cranchia Bonellii* Férussac, 1835) by monotypy.

Histioteuthis elongata (Voss & Voss, 1962)

Figs. 5,a; 7,a; 10; 16

Calliteuthis elongata Voss & Voss, 1962: 184, figs. 4a-f, 6a.—Clarke, M. R., 1966: 198.

Calliteuthis reversa, Joubin, 1900: 96.

Material Examined.—HOLOTYPE: 1 ♀, ML (=GL) 183.0 mm, ATLANTIS, 39°21'N, 70°41'W, 24 July 1940, surface, MCZ 224813.

PARATYPES: 1 ♀, ML (=GL) 175.0 mm, ALBATROSS Sta. 2173, 37°57'N, 72°34'W, 21 July 1884, surface, YPM 12440.—1 ♀, ML (=GL) 166.0 mm, ALBATROSS Sta. 2687, 39°46'N, 71°19'W, 18 July 1886, surface, USNM 78083.—1 sex ?, ML approx. 160 mm, PRINCESSE-ALICE Sta. 1110, 43°21'N, 7°18'15"E, 22 May 1901, surface, IOM.—1 ♀, ML (=GL) 114.0 mm, ATLANTIS, 38°12'N, 70°55'W, 2 Aug. 1935, surface, MCZ 224811.

OTHER MATERIAL: 1 ♀, ML (=GL) 177.0 mm, ALBATROSS Sta. 2687, 39°46'N, 71°19'W, 18 July 1886, surface, YPM 12438.—1 sex ?, ML approx. 145 mm, PRINCESSE-ALICE Sta. 763, 43°30'N, 5°30'E, 14 May 1897, surface, IOM.—1 mantle, ML (=GL) 117+ mm, ALBATROSS Sta. 2180, 39°29'N, 71°49'30"W, 23 July 1884, USNM 39920.—1 sex ?, ML 110+ mm, ALBATROSS Sta. 2039, 38°19'N, 68°20'20"W, 28 July 1883,

USNM 38253.—1 ♀, ML 94+ mm, MMF 9795, Fish Market, Funchal, Madeira, Sept. 1956, from stomach of *Aphanopus ferox*.—1 ♀, ML approx. 88 mm, A. T. CAMERON, set 132-6156, east of Funk Island, Nfld., 28 May 1963, 640 meters.—1 head, ALBATROSS Sta. 2173, 37°57'N, 72°34'W, 21 July 1884, surface, YPM 12440.

Description.—Poor condition of all specimens necessitated use of length of gladius as approximate mantle length, indicated by "ML (=GL)."

Entire animal flaccid. *Mantle* exceptionally long and slender; length three to four times width in specimens of 114.0-183.0 mm ML (=GL). Posterior half of mantle tapers to blunt point. Anteroventral margin slightly excavated medially with obtuse lateral angles.

Fins relatively small, semicircular, leathery in appearance; lobes unite with central notch short distance distal to posterior tip of mantle.

Mantle cartilage of *funnel-mantle locking apparatus* a slightly crescent-shaped ridge, anterior portion strong and cartilaginous, posterior portion fleshy; funnel cartilage with deep medial groove.

Dorsal member of *funnel organ* inverted V-shaped pad with long, narrow arms; papilla at anterior apex; arms appear to have heavy medial ridge down approximately two-thirds their length; ridges appear to merge anteriorly. Two ventral pads long, roughly boomerang-shaped, broader anteriorly than posteriorly. *Valve* semicircular.

Because of exceptionally long mantle, *head* in comparison not disproportionately large as in other histioteuthids; width does not appear to exceed that of mantle. Head not grossly asymmetrical. Left eye appears only about one-quarter larger than right; *sinus* in anterior margin of eyelids. *Nuchal folds* not apparent. *Olfactory organ* fleshy, leaf-shaped knob.

Buccal membrane seven-membered; seven support attachments as follows: first support bifurcate to dorsal sides of arms I; second supports bifurcate to ventral side of I and dorsal side of II, third supports to ventral side of III; fourth supports to dorsal side of IV. *Inner web* low between arms I, II, and III; *outer web* not developed.

Length of *arms* less than that of mantle in sizes studied. Arms relatively stout basally, tapering to slender tips, subequal in length. Single intact arm III with stout, low *swimming keel* on middle third of arm, thereafter reduced to low ridge continuing to distal tip of arm. Distal two-thirds of arms I and II with low keels.

Arm *suckers* on low pedicels; suckers of IV three to four times smaller than those of other arms, approximately coequal in size except for minute ones at tip. Suckers of I, II, and III largest in third quarter of arm, thereafter decreasing abruptly to minuteness. *Horny sucker rings* of IV with numerous low square teeth on either distal or entire margin; sucker rings of I, II, and III smooth except for those of distal quarter of arm; rings of

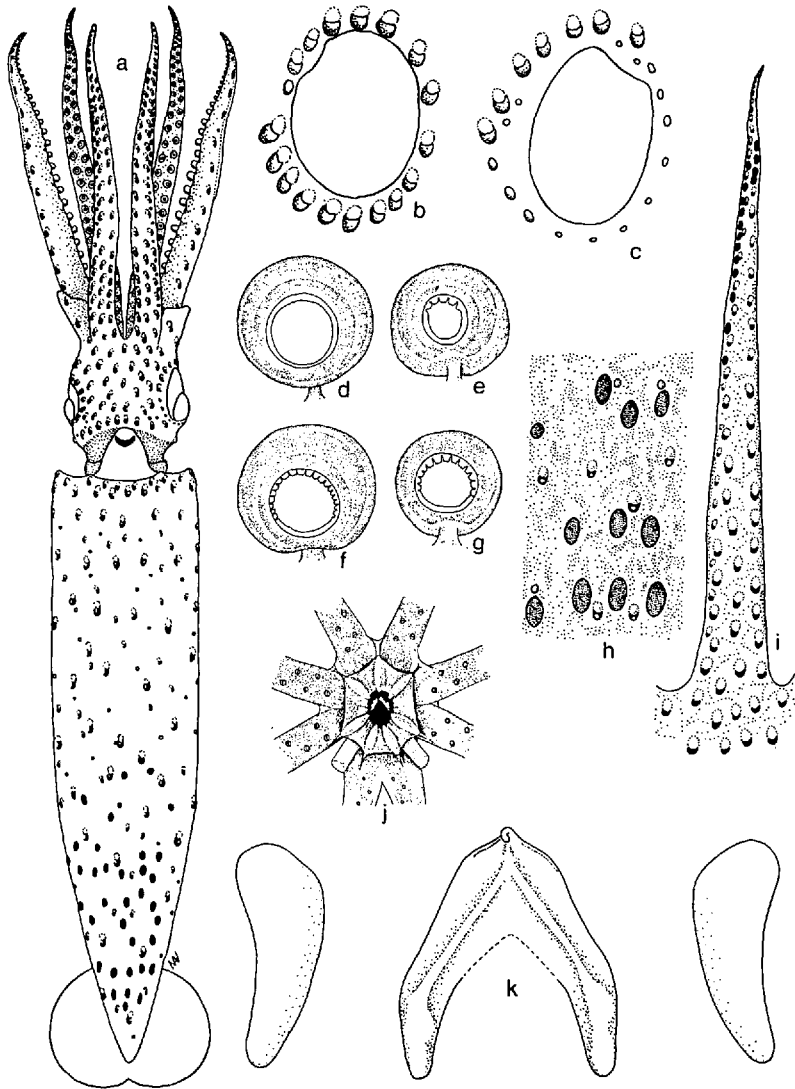


FIGURE 10. *Histiototeuthis elongata* (Voss & Voss, 1962): a, ventral view of holotype, ML 183.0 mm; b, right eyelid of holotype; c, left eyelid of holotype; d, sucker, 10th row of first arm of paratype, YPM 12440; e, sucker, 22nd row of first arm of same; f, sucker, seventh row of fourth arm of same; g, sucker, 20th row of fourth arm of same; h, section of skin from posterior portion of ventral surface of mantle; i, right arm IV of paratype, USNM 78083; j, buccal view, composite drawing; k, funnel organ.

latter suckers with few to numerous small, blunt teeth on distal margin. Low *protective membrane* on each side of double row of suckers.

Tentacles missing on all specimens.

Photophores on ventral surface of mantle numerous, of several types—large and small compound organs, and unique large flat, oval or round, solid black organs which lack the large anterior lens typical of the other photophores. Large compound photophores arranged roughly in about seven diagonal rows extending to near posterior tip of mantle; small photophores scattered in between large organs; posterior third of mantle covered with unique large black photophores described above. Anterior marginal row of photophores on ventral surface continuous with that on dorsal surface of mantle. Dorsal surface with fewer and smaller photophores; unique black photophores not present.

Dorsal surface of head with mostly small photophores widely and regularly set, and few large organs. On ventral surface of head, posterior marginal row with eight large photophores, all but two on the right side. Eighteen photophores, 17 large and one small, in a closed circlet around the right eyelid; seven large photophores in arc over anterior margin of left eye with about 11 small organs continuing around posterior and dorsal margins thereby forming complete circlet with additional few small light organs usually present between circlet and more immediate anterior margin of eyelid. Remaining large photophores in diagonal rows about equally distributed over right and left sides.

Base of arm IV with four longitudinal rows of photophores, three rows of large organs, and one dorsal marginal row of small organs. Dorsalmost row of large photophores with five to six organs extends less than one-third length of arm. At about midarm, small photophores of marginal row replaced by unique black photophores similar to those on posterior part of ventral surface of mantle; row ends short of distal tip of arm as does ventral row of large photophores, distalmost portion of latter row with unique black photophores. Typically, only median row of large photophores extends to distal tip of arm. Arms I, II, and III with ventral row of large photophores to tip; dorsal row of small organs present; several of unique black photophores in terminal portion of ventral row; additional scattered small organs on basal third of arms.

Description of *male genitalia*, *spermatophores*, and *hectocotylization* must await acquisition of male specimen.

Gladius long, thin, translucent, strongly concave on ventral surface. Vane long, 79.7-84.5 per cent of gladius length; slender, 12.9-13.3 per cent of gladius length in pens of 177.0 and 183.0 mm lengths, respectively; tapering margins slightly thickened and pigmented. Rhachis with strongly pigmented lateral margins, terminating posteriorly in coil.

Lower *beak* with mere suggestion of median ridge on lateral wall.

TABLE 1

MANTLE MEASUREMENTS (IN MM) AND INDICES OF *Histioteuthis elongata* (VOSS & VOSS, 1962)

	Holotype MCZ 224813 ♀	Paratypes		
		YPM 12440 ♀ gravid	USNM 78083 ♀ gravid	MCZ 224811 ♀ gravid
ML (= GL)	183	175	166	114
MWI	24.6	24 (approx.)	29.5	33.3
HLI	16.4	—	20.5	—
HWI	16.4	—	—	25.4
FLI	19.0	18.6	21.1	28.1
FWI	26.8	26.9	27.1	32.9
AI I	50.0	—	60.0	87.7
II	50.8	—	—	—
III	—	—	71.0	—
IV	44.8	45.7	71.0	—
TLI	—	—	—	—
CLI	—	—	—	—
M+I	4.1	4.0	2.4	6.2

Radula of a specimen from off the northeast coast of United States illustrated. First and second laterals only slightly asymmetrical. No marginal plates present.

Type.—Museum of Comparative Zoology, MCZ 224813.

Type-Locality.—Western North Atlantic, 32°21'N, 70°41'W.

Discussion.—*Histioteuthis elongata* is certainly the most unhistioteuthid-like member of the family with its long slender mantle and more symmetrical head. It can be immediately distinguished from all other known members of the family by these unique characters plus the presence of the peculiar large black photophores, described earlier, on the ventral surface of the mantle and the distal portions of the arms. The tentacles and clubs from more complete specimens may in the future yield additional distinctive characters.

Though all of the suckers of arms I, II, and III, except for those on the distal quarter of the arm, were smooth in the available material, it would be within the range of variation characteristic of the family to find toothed suckers, if more specimens were available.

Growth is accompanied by significant proportional changes; the mantle becomes proportionately longer, and the fins, head, and arms proportionately smaller.

Remarks.—The original ten specimens were all found floating on the surface, either dead or dying. They were in poor condition, all mutilated,

obviously by having been fed upon by predators. Though collected over a period of many years, all of the western Atlantic specimens were found within a few degrees of each other during the months of July and August. Similarly, the two Mediterranean specimens, collected years apart, were within two degrees of each other and both were taken in the month of May. As discussed in the original work (Voss & Voss, 1962), the available data for these specimens suggests a causative hydrographic condition, possibly areas of upwelling (seasonal?) wherein the normally deep-dwelling animal is brought to the surface and there preyed upon. Another possibility is that they had been regurgitated by one of the large predators.

Distribution.—One newly acquired specimen of *elongata* recovered from the stomach of an *Aphanopus ferox* from the Fish Market in Funchal, Madeira, and one or possibly two specimens taken in waters east of Newfoundland by trawls fished at 640 and 732 meters (Mercer, in manuscript) augment the distribution records for this species. To date, it is known in the North Atlantic from off the northeastern coast of North America and from the vicinity of the Madeira Islands and in the Mediterranean Sea. While present in the upper 700 meters, the depth range of this species is unknown, since most of the material has been found floating at the surface.

Histioteuthis reversa (Verrill, 1880)

Figs. 3, f-h; 5, b; 7, b-c; 11; 12; 14, a-h

Calliteuthis reversa Verrill, 1880a: 393; 1880b: 362; 1881a: 295, pl. 46, figs. 1-1b; 1881b: 112, pl. 7, figs. 1-1b; 1882a: 327, pl. 22, figs. 1-1c; 1884: 243.—?Russell, 1909: 455.—?Chun, 1914: 5.—Naef, 1923: 352, text-figs. 173-180.—Johnson, 1934: 162.—G. Voss, 1958: 383 (in part: only specimen from station RHB 450).—Morales, 1958: 23.—Adam, 1960: 485.—Voss & Voss, 1962: 169.—Clarke, M. R., 1962b: 439, 449.—Torchio, 1965: 266, fig. 1.—Clarke, M. R., 1966: 196, fig. 39.

Calliteuthis Meneghinii, Pfeffer, 1912: 250, pl. 20, figs. 1, 8-10, pl. 21, figs. 1, 9-11, pl. 22, figs. 13-19 (not *Loligo Meneghinii* Verany, 1851: 98, pl. 35, figs. c,d,e).—Joubin, 1924: 68 (in part: only specimens from stations 3281, 3285, 3473, 3591).—Degner, 1925: 20.—Torchio, 1962: 32, text-figs. 1-2.

Stigmatoteuthis Verrilli Pfeffer, 1912: 285.—Johnson, 1934: 162.

Stigmatoteuthis Chuni, Joubin, 1920: 55, pl. 13, fig. 3 (not *Stigmatoteuthis Chuni* Pfeffer, 1912: 286).

Calliteuthis reversa var. *mediterranea* Naef, 1921: 541.

Calliteuthis reversa var. *atlantica* Grimpe, 1922: 47.

Calliteuthis (*Stigmatoteuthis*) *Verrilli*, Joubin, 1924: 71 (in part: only specimens from stations 3412, 3414, 3447, and 3453).

Material Examined.—HOLOTYPE OF *Calliteuthis reversa*: 1 ♀, ML 51.0 mm, FISH HAWK Sta. 894, 39°53'N, 70°58'30"W, 666 meters, USNM 574849.

HOLOTYPE OF *Stigmatoteuthis Verrilli*: 1 sex ?, ML 27 mm, ALBATROSS Sta. 2076, 1883, 1659 meters, YPM 12442.

OTHER MATERIAL: 1 ♂, ML approx. 61 mm, DELAWARE Sta. 62-11, tow 14, 42°43'N, 63°43'W, 2 Oct. 1962, 740-960 meters.—1 ♀, ML 54.8 mm, DELAWARE Sta. 62-11, tow 13, 42°46'N, 63°39'W, 2 Oct. 1962, 548-750 meters.—1 ♂, ML 49 mm, A. T. CAMERON, off Newfoundland, 8 Nov. 1962, 732 meters.—3 ♀♀, ML 40.5-17.3 mm, GALATHEA Sta. 137, 20°04'S, 11°56'E, 23 Dec. 1950, mw 1000.—2 ♂♂, ML 38.6-29.0, DELAWARE 63-4 Sta. 7, 41°27'N, 27°35'W, 4 May 1963.—1 ♀, ML 30.0 mm, UNDAUNTED 66-3, Sta. 17, 31°32.4'N, 68°34.8'W, 12 May 1966, 0-1302 meters.—1 ♀, ML 14.3 mm, ALBATROSS III Cruise 120, 39°45.3'N, 71°14.8'W, 28 Oct. 1958, mw 914.—3 spec., ML 13.0-10.5 mm, off west coast of Africa, coll. Dr. Rancurel.—1 spec., ML 28.6 mm, DANA Sta. 4171 V, 45°12'N, 18°27'W, 31 May 1931, mw 300.—1 ♀, ML 28.0 mm, DANA Sta. 1380 III, 36°26'N, 21°41'W, 19 June 1922, mw 600.—1 ♀, 1 ♂, ML 27.0-23.4 mm, DANA Sta. 4158 IX, 46°28'N, 8°01'W, 18 June 1930, mw 300.—1 ♀, ML 27.0 mm, DANA Sta. 4157 I, 44°01'N, 9°13'W, 16 June 1930, mw 1000.—1 ♀, ML 20.0 mm, DANA Sta. 4173 III, 40°46'N, 18°35'W, 3 June 1931, mw 400.—1 ♀, ML 19.0 mm, DANA Sta. 4172 II, 43°05'N, 18°05'W, 1 June 1931, mw 500.—3 ♀♀, ML 18.2-12.0 mm, DANA Sta. 4007 III, 18°22'N, 18°14'W, 15 March 1930, mw 300.—1 spec., ML 17.8 mm, DANA Sta. 4007 IV, 18°22'N, 18°14'W, 15 March 1930, mw 100.—1 spec., ML 16.8 mm, DANA Sta. 1342 IV, 34°00'N, 70°01'W, 15 May 1922, mw 2000.—1 spec., ML 16.0 mm, DANA Sta. 4194 VIII, 41°56'N, 30°08'W, 22 June 1931, mw 300.—1 ♀, ML 14.7 mm, DANA Sta. 1385 V, 43°10'N, 9°50'W, 24 June 1922, mw 200.—1 spec., ML 14.4 mm, DANA Sta. 1171 IV, 8°19'N, 44°35'W, 13 Jan. 1921, mw 300.—1 ♀, ML 14.0 mm, DANA Sta. 4007 VI, 18°22'N, 18°14'W, 15 March 1930, mw 4000.—1 spec., ML 13.8 mm, DANA Sta. 4003 V, 8°26'N, 15°11'W, 9 March 1930, mw 2000.—1 ♀, ML 13.5 mm, DANA Sta. 4007 VII, 18°22'N, 18°14'W, 15 March 1930, mw 3500.—1 spec., ML 13.0 mm, DANA Sta. 4193 I, 41°37'N, 27°00'W, 20 June 1931, mw 500.—1 ♀, ML 13.0 mm, DANA Sta. 4007 XI, 18°22'N, 18°14'W, 15 March 1930, mw 1000.—1 spec., ML 12.9 mm, DANA Sta. 1385 I, 43°10'N, 9°50'W, 24 June 1922, mw 1000.—1 spec., ML 12.9 mm, DANA Sta. 1166 III, 10°16'N, 40°41'W, 11 Nov. 1921, mw 600.—1 spec., ML 12.1 mm, DANA Sta. 4025 V, 35°57'N, 5°30'W, 9 April 1930, mw 500.—1 ♀, ML 12.0 mm, DANA Sta. 4200 III, 45°55'N, 29°01'W, 27 June 1931, mw 150.—1 spec., ML 11.7 mm, DANA Sta. 4003 X, 8°26'N, 15°11'W, 9 March 1930, mw 100.—1 spec., ML 11.4 mm, DANA Sta. 1386 VII, 45°15'N, 8°43'W, 24 June 1922, mw 50.—2 spec., ML 11.0-8.4 mm, DANA Sta. 4017 IV, 29°11'N, 14°14'W, 23 March 1930,

mw 2000.—2 spec., ML 11.0 to approx. 4.0 mm, DANA Sta. 1272 II, 17°43'N, 64°56'W, 23 March 1922, mw 600.—2 spec., ML 10.9-6.9 mm, DANA Sta. 4008 IV, 21°40'N, 18°00'W, 16 March 1930, mw 100.—10 spec., ML 10.5-6.3 mm, DANA Sta. 4203 III, 49°49'N, 30°22'W, 30 June 1931, mw 300.—4 spec., ML 10.2-2.3 mm, DANA Sta. 4201 XX, 47°02'N, 31°45'W, 28 June 1931, mw 2000.—1 spec., ML 10.0 mm, DANA Sta. 4008 III, 21°40'N, 18°00'W, 16 March 1930, mw 300.—6 spec., ML 9.5-3.5 mm, DANA Sta. 4201 XIV, 47°02'N, 31°45'W, 28 June 1931, mw 100.—3 spec., ML 9.4-6.0 mm, DANA Sta. 4005 XI, 13°31'N, 18°03'W, 12 March 1930, mw 50.—2 spec., ML 9.2-8.8 mm, DANA Sta. 4203 IV, 49°49'N, 30°22'W, 30 June 1931, mw 100.—1 spec., ML 8.6 mm, DANA Sta. 4014 III, 28°09'N, 15°19'W, 25 March 1930, mw 900.—2 spec., ML 8.3-6.6 mm, DANA Sta. 4005 X, 13°31'N, 18°03'W, 12 March 1930, mw 100.—1 spec., ML 8.3 mm, DANA Sta. 1102 V, 47°15'N, 7°25'W, 8 Sept. 1921, mw 150.—1 spec., ML 8.0 mm, DANA Sta. 4065 III, 35°22'N, 19°28'E, 13 May 1930, mw 600.—1 spec., ML 8.0 mm, DANA Sta. 4205 VI, 51°48'N, 30°30'W, 1 July 1931, mw 50.—1 spec., ML 7.9 mm, DANA Sta. 1293 II, 17°43'N, 64°56'W, 17 April 1922, mw 800.—1 spec., ML 7.6 mm, DANA Sta. 4070 III, 35°40.5'N, 21°54'E, 16 May 1930, mw 4000.—1 spec., ML approx. 7.4 mm, DANA Sta. 4001 III, 3°56'N, 12°32.5'W, 6 March 1930, mw 300.—1 spec., ML 6.9 mm, DANA Sta. 1186 V, 17°54'N, 64°54'W, 30 Nov. 1921, mw 1000.—2 spec., ML 6.9-5.9 mm, DANA Sta. 4202 II, 47°36'N, 28°39'W, 29 June 1931, mw 200.—4 spec., ML 6.5-4.1 mm, DANA Sta. 4203 III, 49°49'N, 30°22'W, 30 June 1931, mw 300.—9 spec., ML 6.5-2.7 mm, DANA Sta. 4201 XV, 47°02'N, 31°45'W, 28 June 1931, mw 50.—1 spec., ML 6.3 mm, DANA Sta. 1103 I, 45°46'N, 8°56'W, 9 Sept. 1931, mw 300.—1 spec., ML 6.3 mm, DANA Sta. 1157 XIII, 21°57'N, 22°58'W, 27 Oct. 1921, mw 500.—1 spec., ML 6.2 mm, DANA Sta. 4194 IX, 41°56'N, 30°08'W, 22 June 1931, mw 200.—1 spec., ML 5.7 mm, DANA Sta. 4005 III, 13°31'N, 18°03'W, 12 March 1930, mw 3000.

Description.—Mantle conical, moderately elongate with gently tapering sides terminating posteriorly in blunt point; walls moderately heavy. Median anterodorsal margin produced to form low obtuse angle; anteroventral margin slightly excavated without sharp lateral angles.

Fins small, thin, transversely oval, united posteriorly with median notch. Fins extend slightly posterior to free tip of mantle.

Funnel with two dorsal supports. *Funnel-mantle locking apparatus* typical, crescent-shaped mantle member narrow but strong anteriorly, broad posteriorly; funnel cartilage elongate oval, narrower anteriorly, with median groove deep anteriorly and shallow and broad posteriorly. Dorsal member of *funnel organ* inverted V-shaped with anterior apical papilla

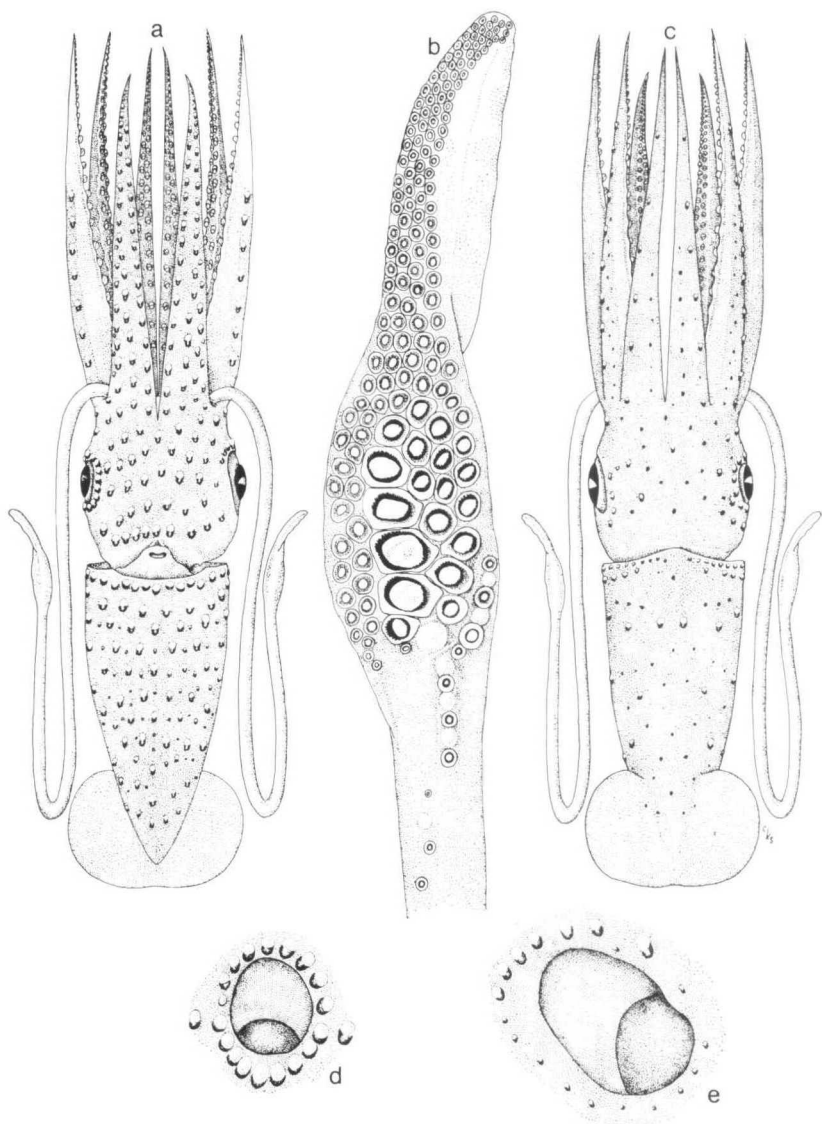


FIGURE 11. *Histioteuthis reversa* (Verrill, 1880): a, ventral view, *Del* 63-4 Sta. 7, ML 38.6 mm; b, right tentacular club, *Del* 63-4 Sta. 7, ML 29.0 mm; c, dorsal view, *Del* 63-4 Sta. 7, ML 38.6 mm; d, right eyelid, *Del* 63-4 Sta. 7, ML 29.0 mm; e, left eyelid of same.

and long narrow arms; median two-thirds of each arm with low longitudinal ridge originating independently posterior to papilla (ridge may be obscured if pad is swollen); two ventral pads kidney-shaped. *Funnel valve* semicircular.

Head large, wider than mantle. Left *eye* about twice size of right; *sinus* in anterior margin of eyelids. One or two weak *nuchal folds* present on each side of head. *Olfactory organ* bar-like knob.

Buccal membrane seven-membered; seven support attachments as follows: first support bifurcate to dorsal sides of arms I; second supports to dorsal sides of II; third supports to ventral sides of III; fourth supports to dorsal sides of IV. *Inner web* low to vestigial between dorsal three pairs of arms; *outer web* not conspicuously developed.

Arms strong, heavy in basal third, tapering to slender tips; approximately one to one and a half times length of mantle. Arms II and III subequal, longer than subequal arms I and IV; arm formula $2 = 3.1 = 4$. *Swimming keel* on III originates at midarm, expands, then reduces to low ridge continuing to tip of arm; distal thirds of arms I and II with low keels. Orally, *protective membranes* developed on basal third or half of arms.

Suckers of arms IV about one-third size of those of other arms; suckers of I, II, and III in small specimens usually with four to ten low, broad, blunt or pointed teeth on distal margin with proximal margin smooth, in larger specimens entire margin usually smooth; distalmost suckers often more distinctly toothed.

No *hectocotylyzation* apparent in available male specimens.

Tentacles one and a half to two times length of mantle. *Club* expanded, with median low swimming keel on distal half of aboral surface; deep longitudinal *cleft* may or may not be present on proximal half. *Carpal adhesive apparatus* extends approximately two to three club lengths proximal to club on oral surface of tentacular stalk. In single row along ventral margin of stalk, arrangement from this distal point is as follows: 1 p, then widely spaced alternating pairs of suckers and pads (2 s, 2 p, 2 s, 2 p, etc.). Proximal to club, row crosses over with paired elements diagonally set, then arrangement continues in single row in 1 p, 1 s, 1 p, 1 s arrangement terminating at base of manus in enlarged pad, three to four times size of other carpal elements in large individuals. Three pairs of alternating suckers and pads continue up proximal margin of manus. Above description from left tentacle of western North Atlantic specimen. Typically, arrangement might occur on right tentacle in some individuals with mirror image on left. Occasional carpal element on tentacular stalk may be lacking.

Tentacular suckers in about six diagonal rows, then in five and four on dactylus. On manus, suckers of median two rows enlarged, especially central four or five of more ventral of two rows; in large individuals,

enlarged three to four times over other suckers. On dactylus, suckers uniform, gradually decreasing in size.

Protective membrane on each side of club, dorsal one decreasing distally, terminating at approximately two-thirds club length; ventral one reducing as club narrows, continuing to distal tip.

Horny rings of suckers of manus usually with numerous straight-sided, blunt or pointed teeth on entire margin; teeth often heavier and less closely set on proximal margin. Some specimens with very irregular dentition on enlarged central suckers; some with these sucker rings nearly smooth.

Photophores numerous on ventral surface of mantle, both large and small organs regularly intermixed to near distal tip. Large photophores in about seven diagonal rows; photophores fewer, more widely spaced on dorsal surface of mantle. Large photophores numerous on ventral surface of head, regularly set in diagonal rows with exception of ring around margins of eyelid; seven or eight organs in posterior marginal row. Eighteen photophores, 17 large and one small, in closed circlet around right eyelid; (occasional specimen with 19 photophores, 18 large and one small); seven large light organs in arc over anterior margin of left eyelid with 10 to 14 small organs regularly spaced around remaining margin of eyelid.

Arms IV with four longitudinal rows of photophores, three of large and a dorsal marginal row of small organs; latter row terminates at approximately one-half length of arm; dorsalmost row of large photophores, with five to eight organs, terminating at approximately midarm; ventral row terminating short of tip of arm with only median row of large photophores extending to tip. Arms III, II, and I with two to three longitudinal rows of photophores with only ventral row of large organs extending to tip.

Male genitalia single, on left side. Mature *spermatophores* found in three males of sizes 49, 61, and 90 mm ML. Spermatophore length varied from 2.4 to 3.82 mm (SpLI 0.033-0.055). Ejaculatory apparatus short (EjAI 12.1-17.5 in western Atlantic specimens, 18.3-20.7 in eastern Atlantic specimen), with single large central loop. Cement body long (CBI 73.0-81.7 in western Atlantic specimens, 39.2-47.3 in eastern Atlantic specimen); oral connective complex with low fleshy collar and broad shallow cavity, constriction and more granular nature further delineates this oral portion. Sperm mass short in western Atlantic males (SpMI 5.6-10.8), moderately long in eastern Atlantic male (SpMI 33.5-36.8).

Gladius delicate, ventral surface deeply concave. Vane long, GVLI 70.0-73.3, moderately broad, GVWI 26.2-25.8, in 41.0- and 49.0-mm-ML specimens, respectively. Posteriorly tapering lateral margins of vane slightly thickened and pigmented. Rhachis with lateral margins heavily pigmented; terminates posteriorly in coil.

Lower beak with weak median ridge on lateral wall.

Radulas of two specimens from off Blanes, Spain, illustrated. First and

second laterals asymmetrical, and of increasing length. Weak tear-shaped marginal plates present in one specimen.

Type.—United States National Museum, USNM 574849.

Type-Locality.—Western North Atlantic, 39°53'N, 70°58'30"W, 666 meters.

Discussion.—In the redescription of *Calliteuthis reversa* Verrill (Voss & Voss, 1962), the status of the species was discussed in detail. Verrill's type was examined together with his later specimen (1884) (designated by Pfeffer, 1912, as type for his species *Stigmatoteuthis Verrilli*) which had intact tentacles, a feature lacking in the type. It was concluded without doubt that neither *Calliteuthis Meneghinii* (Verany) nor *Stigmatoteuthis Verrilli* Pfeffer could be considered valid species; *Calliteuthis Meneghinii* was relegated to the status of a *species dubia* and *Stigmatoteuthis Verrilli* placed into the synonymy of *reversa*.

Pfeffer's two large specimens, on which he actually based his description of *Calliteuthis Meneghinii* in his 1912 monograph, were sought at the Leipzig Museum and the Würzburg Museum, Pfeffer's stated source of the material. I was unsuccessful in obtaining any information from Leipzig, and correspondence with Prof. Dr. E. Rutte, Johannes Gutenberg University, Mainz, revealed that the Würzburg Museum no longer exists, the collections having been largely destroyed in World War II. Thus Pfeffer's material was unavailable for study. In the light of the large number of histioteuthids that I have studied, I consider the chitinous accessory structures on the tentacular club suckers described by Pfeffer to be aberrancies, which do occur in the family. In every other respect, Pfeffer's description fits that of *reversa*.

Since it is seen that the rings of the arm and tentacular suckers may be toothed and that accessory chitinous structures on the tentacular suckers do not exist in the species except possibly as an aberrancy, then the resultant confusion introduced by Pfeffer in separating *Stigmatoteuthis* and *Calliteuthis* has been clarified.

The species *H. reversa* is well characterized and may be distinguished from the other species of the genus by the following combination of characters: intermixed large and small photophores on entire ventral surface of mantle; four longitudinal rows of photophores on arms IV; 18 photophores (17 large and one small) around the right margin of the eyelid, a closed circlet of 10-14 small photophores around the left margin of the eyelid, in addition to the arc of large photophores over the anterior margin; and the median longitudinal ridges on the arms of the dorsal pad of the funnel organ.

Typically, considerable variation is found in the dentition of the rings of the suckers of arms I, II, and III. Though most of the small specimens

TABLE 2
MANTLE MEASUREMENTS (IN MM) AND INDICES OF *Histioteuthis reversa* (VERRILL, 1880)

	♂ Del 62-11	♂ Holotype 574849	D 4171 V	D 1380 III	♂ D 4157 I	♂ D 4173 III	♂ D 4007 III	D 4194 VIII	♂ D 4007 VI	*	D 4025 V	*
ML	54.8	51.0	28.6	28.0	27.0	20.0	18.2	16.0	14.0	13.0	12.1	11.5
MLI	—	—	38.2	35.9	—	35.7	37.9	37.2	37.4	39.5	39.3	38.3
MWI	42.0	39.2	50.3	56.8	48.2	55.5	52.2	62.5	58.5	59.2	56.2	63.5
HLI	—	31.4	40.9	49.3	44.5	62.5	51.6	51.8	55.0	53.8	47.2	52.2
HWI	—	41.2	53.5	60.0	48.2+	55.5	50.5	62.5	62.9	72.4	60.3	73.0
FLI	43.7	33.4	40.9	43.2	38.9	50.0	39.5	50.0	52.8	56.9	53.7	55.6
FWI	59.3	47.0	69.2	67.9	55.5	72.5	62.1	75.0	79.3	82.2	83.5	87.0
IV I	—	113.9	104.1	95.6	92.5	105.0	90.7	75.7	89.5	86.1	91.0	88.7
III	140.6	131.3	109.3	114.2	100.0	115.0	93.5	100.7	98.5	89.1	96.8	99.0
II	143.7	133.2	112.2	104.6	103.0	115.0	97.9	93.7	99.4	92.3	99.4	95.5
IV	107.8	117.8	98.0	98.2	89.0	100.0	79.7	73.7	83.5	76.9	84.4	87.0
TLI	235.0	—	171.3	209.9	185.0	203.0	138.9	131.2	153.7	115.3	124.0	174.9
CLI	32.6	—	29.0	30.4	27.8	30.0	27.4	25.0	27.2	23.1	26.4	23.5
M+I	7.7	—	10.5	14.3	7.4	10.0	14.8	14.4	21.4	17.7	16.5	17.4

* Specimens collected off west coast of Africa by P. Rancurel.

had the described four to ten teeth on the distal margin of the rings, some had as many as twenty-five on the entire margin. Most of the larger specimens lacked any dentition at all (with the exception of the terminal suckers) as does Verrill's type-specimen.

Somewhat similarly, the dentition of the rings of the enlarged tentacular suckers varies from regularly toothed margins, to irregular, to almost smooth margins.

Though the general pattern of the carpal apparatus remained constant, a few specimens lacked one or more pads or suckers. Probably because of an artifact of preservation or because of differing stages in activity of the organ, some variation was noted in the longitudinal ridges on the dorsal pad of the funnel organ; they ranged from a normal low ridge to one so high as to appear almost flaplike. In an occasional specimen, the ridges were completely obscured by the swollen state of the organ.

The presence of mature spermatophores in males from both sides of the Atlantic afforded an insight into the variations which may occur in this organ within such a widely distributed species as *reversa*. Though the spermatophores closely resemble each other structurally, proportionately they strongly differ. The most striking difference is in the length of the sperm mass, which is very short in the two western Atlantic males (one from off Newfoundland, the other from off New England), and moderately long in the eastern Atlantic male (from off the Spanish coast). The number and position of the large coils in the sperm mass of this latter specimen were not consistent within the same lot of spermatophores and could possibly be due to preservation. Again, more material is necessary before any sound conclusions may be drawn, but it certainly suggests the occurrence of two separate breeding populations.

In well-preserved specimens as small as 5.3 mm ML, most of the definitive photophore pattern is discernible by telltale dark, usually round, chromatophores overlying the base of the developing light organ. In specimens under about 8 mm ML, the small photophore in the 18-photophore pattern around the right eyelid is not always distinguishable, but the vacant space for it is obvious. The dorsal marginal row of small photophores on arm IV is difficult to discern in specimens smaller than about 14 mm ML but the photophore count in the dorsalmost row of large photophores is distinct.

Contributions to the postembryological development of *reversa* have been made by Naef (1923) and Degner (1925).

Data in Table 2 are from the holotype and certain specimens of particular interest secured since the redescription of *reversa* by Voss & Voss (1962); in the redescription may be found the data for forty specimens (including those reported on by Joubin [1900, 1920, 1924]) ranging in size from 5.3

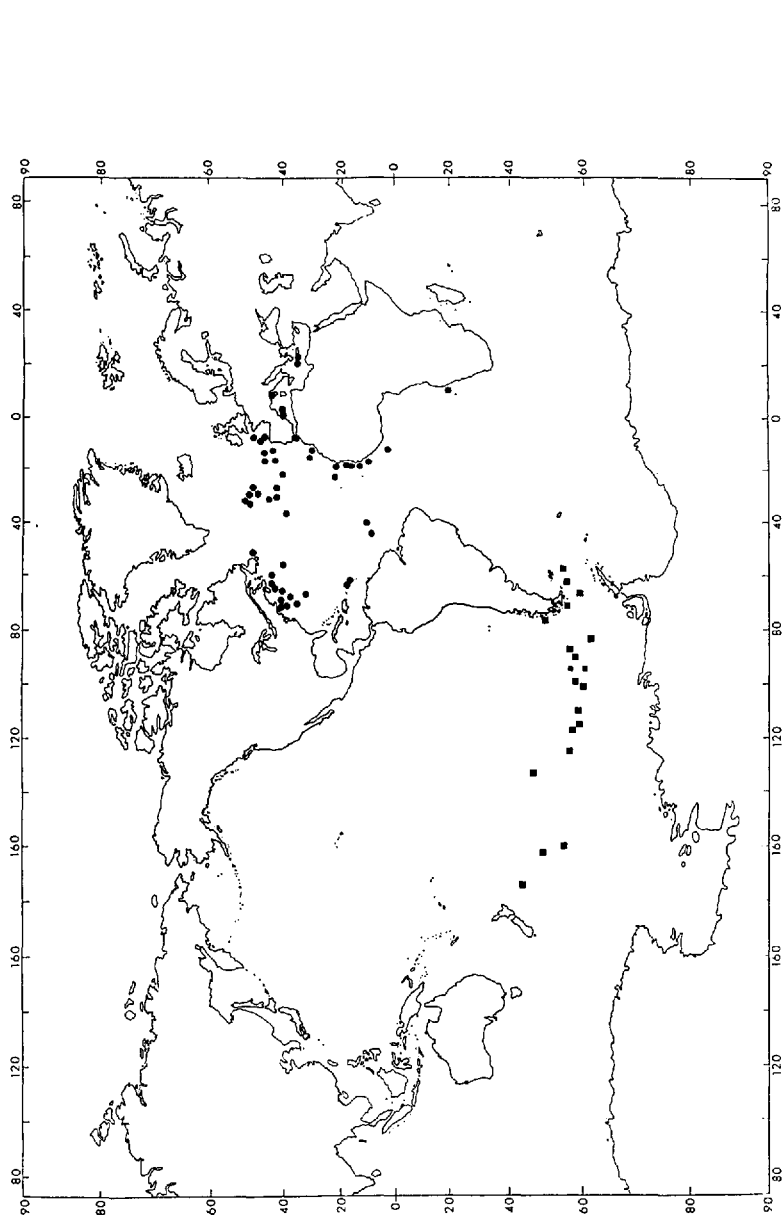


FIGURE 12. Distribution of confirmed, identified specimens. ● = *Histioteuthis reversa* (Verrill); ■ = *H. eltaninae*, n. sp.

to 90.0 mm ML. These latter specimens were included in the present study but the republication of their data was not thought necessary.

Distribution.—Additional material has greatly expanded the known distribution of *reversa* to include now the major part of the North Atlantic south of approximately 55° latitude, including the Mediterranean but excluding the Gulf of Mexico. With the extensive trawling done in the Gulf of Mexico and the Caribbean, *reversa* has been noticeably absent, represented in the Caribbean area only by four juveniles taken by the DANA in the vicinity of the Virgin Islands. Voss & Voss (1962) mistakenly included the Gulf of Mexico in the distribution of this species. *H. reversa* has also been taken in the South Atlantic from off the west coast of Africa south to approximately 20°S latitude.

This species appears to range from surface waters to approximately 1000 meters, and in greatest abundance in proximity to land masses or oceanic ridges.

***Histioteuthis eltaninae*, n. sp.**

Figs. 3, d-e; 5, c; 7, d; 12; 13; 14, i-m

Material Examined.—HOLOTYPE: 1 ♀, ML 53.3 mm, ELTANIN Sta. 1723, 40°05'S, 149°55'W, 18 July 1966, ca. 880 meters, 3-m IKMT, USNM 576164.

PARATYPES: 1 ♂, ML 66.0 mm, ELTANIN Sta. 354-20, 55°25'S, 58°51'W, 5 Dec. 1962, 1812-2145 meters, UMML.—1 ♂, ML 57.3 mm, ELTANIN Sta. 325-20, 56°06'S, 71°14'W, 7 Nov. 1962, 983 meters, USNM 576170.—1 ♂, ML 45.2 mm, ELTANIN Sta. 1270, 57°31'S, 125°16'W, 1 Sept. 1964, 851-933 meters, USNM 576171.—1 ♀, ML 45.0 mm, ELTANIN Sta. 235-20, 59°06'S, 67°59'W, 2 Oct. 1962, 1830 meters, USNM 576172.—1 ♂, ML 39.0 mm, ELTANIN Sta. 1107-13-4, 58°00'S, 90°36'W, 24 May 1964, 714-851 meters, USNM 576173.—1 ♂, ML 35.5 mm, ELTANIN Sta. 110-15, 56°59'S, 62°16'W, 19 July 1962, approx. 2890 meters, USNM 576174.—1 ♂, ML 34.4 mm, ELTANIN Sta. 1100-13-3, 57°07'S, 88°44'W, 22 May 1964, 183 meters, UMML.—1 ♂, ML 29.9 mm, ELTANIN Sta. 1201, 56°14'S, 160°05'W, 8 Aug. 1964, 1120 meters, USNM 576175.

OTHER MATERIAL: 1 ♀, ML 52.4 mm, ELTANIN Sta. 1306, 61°01'S, 100°19'W, 20 Oct. 1964, 1208-1373 meters.—1 ♀, ML 51.1 mm, ELTANIN Sta. 1302, 58°57'S, 99°30'W, 16 Oct. 1964, 769-1336 meters.—1 ♀, ML 47.3 mm, ELTANIN Sta. 792-20, 64°10'S, 82°49'W, 25 Oct. 1964, 1501-1720 meters.—1 ♀, ML 45.0 mm, ELTANIN Sta. 1307, 60°58'S, 100°46'W, 20 Oct. 1964, 1208-1373 meters.—1 ♀, ML 40.3 mm, ELTANIN Sta. 99, 51°43'S, 77°36'W, 12 July 1962, 1208-1219 meters.—1 ♀, ML 37.0 mm, ELTANIN Sta. 1480, 47°14'S, 132°28'W, 4-5 Aug. 1965,

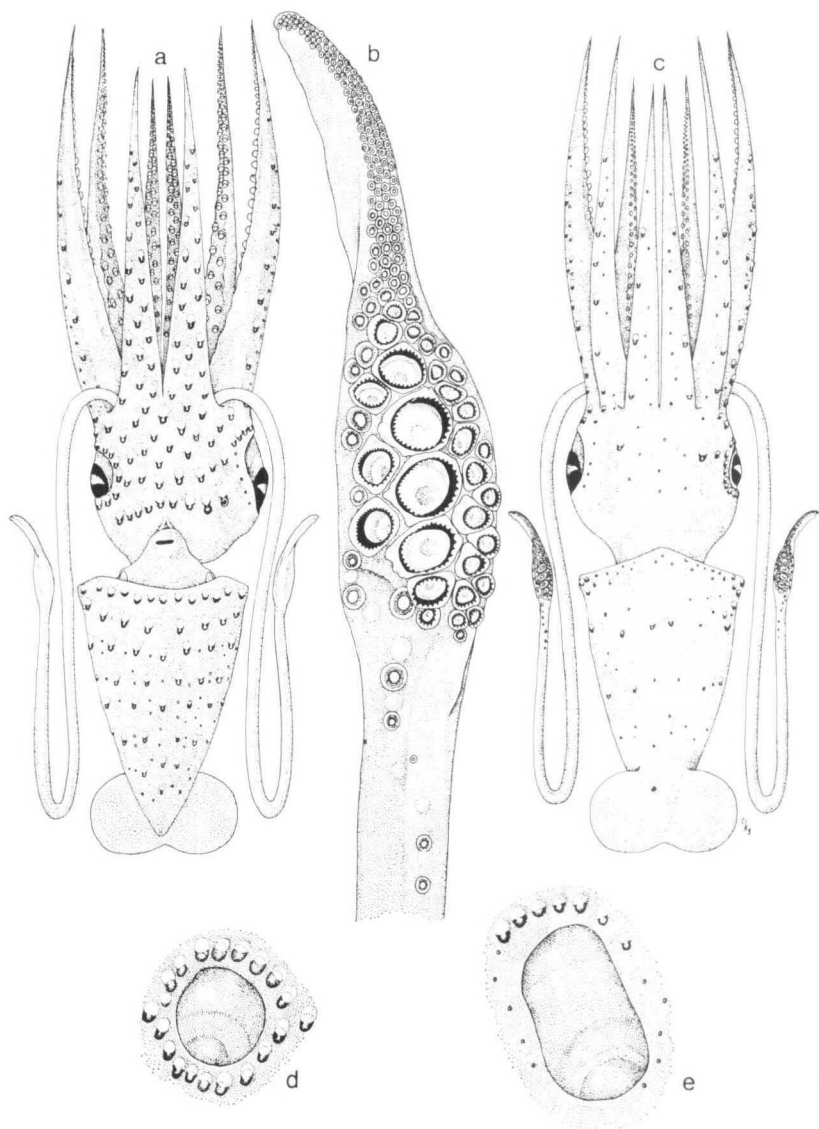


FIGURE 13. *Histioteuthis eltaninae*, n. sp.: a, ventral view of holotype, ML 53.3 mm; b, left tentacular club of paratype, ML 57.3 mm; c, dorsal view of holotype; d, right eyelid of same; e, left eyelid of same.

329 meters, 3-m IKMT.—4 ♀♀, 5 ♂♂, ML 30.9-15.2 mm, ELTANIN Sta. 1686, 57°39'S, 115°12'W, 6 May 1966, 600-750 meters, 3-m IKMT.—1 ♂, ML 28.0 mm, ELTANIN Sta. 1474, 59°00'S, 110°03'W, 25-26 July 1965, 439 meters, 1-m IKMT.—3 ♀♀, 4 ♂♂, ML 27.7-18.5 mm, ELTANIN Sta. 1684, 59°07'S, 114°59'W, 5 May 1966, 300-425 meters, 3-m IKMT.—1 ♀, 2 sex ?, ML 26.9 to approx. 14 mm, ELTANIN Sta. 1687, 57°39'S, 115°26'W, 6 May 1966, 400-1210 meters, 3-m IKMT.—1 ♀, ML 22.9 mm, ELTANIN Sta. 1704, 43°50'S, 174°27'W, 22 May 1966, 725-800 meters, 3-m IKMT.—1 ♂, ML 21.6 mm, ELTANIN Sta. 1473, 58°54'S, 110°04'W, 25 July 1965, 366 meters, 3-m IKMT.—1 ♂, ML 20.0 mm, ELTANIN Sta. 1692, 49°00'S, 161°57'W, 17 May 1966, 0-2300 meters, 3-m IKMT.—1 spec., ML 9.0 mm, ELTANIN Sta. 360-20, 56°29'S, 58°25'W, 7 Dec. 1962, 1603-1885 meters.

Description.—*Mantle* conical, moderately elongate, usually widest at flared-out anterior margin, walls moderately thick. Middorsal anterior margin produced into low obtuse angle; midventral anterior margin slightly excavated between lateral angles.

Fins with free posterior margins extending beyond posterior tip of mantle. Fin width approximately three-quarters to one-half mantle length; length approximately one-third to one-half mantle length.

Funnel with typical double dorsal supports. *Mantle locking apparatus* with long slightly crescent-shaped mantle cartilage fitting into deep central groove of oval funnel cartilage. Dorsal pad of *funnel organ* sculptured with independent median ridge descending each arm and merging into swollen posterior tip; two ventral pads kidney-shaped. Large semicircular *valve* present.

Head typically large, wider than mantle, with asymmetrically enlarged left eye. One *nuchal fold* apparent on either side of head dorsal to small *olfactory organ*.

Buccal membrane seven-membered with support attachments as follows: middorsal or first bifurcate to dorsal sides of arms I, second supports to dorsal sides of II, third supports to ventral sides of III, and fourth supports to dorsal sides of IV. *Inner web* low to vestigial; *outer web* not conspicuously developed.

Arms stout basally, tapering to delicate tips, approximately one to one and one-quarter the length of mantle. Condition of available material inadequate for description of *keels*. Arms II and III about coequal in length, longer than coequal arms I and IV. *Fleshy protective membranes* present, more developed on ventral margins.

Suckers on third quarter of arm slightly larger than on remainder; those on IV considerably reduced in size. Rings with low triangular teeth varying

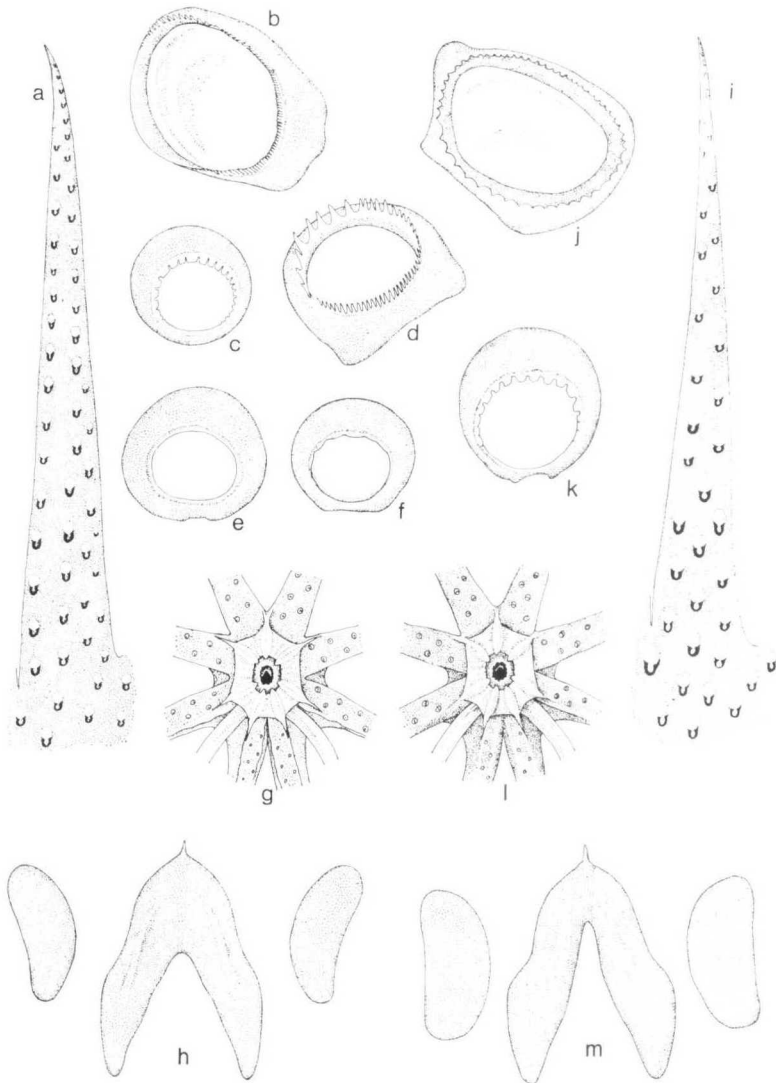


FIGURE 14.—a-h, *Histioteuthis reversa* (Verrill, 1880): a, left arm IV, *Del* 63-4 Sta. 7, ML 38.6 mm; b, largest club sucker from specimen off Blanes, Spain; c, sucker from 13th row, arm IV of same; d, club sucker, ventral row of same; e, sucker from 13th row, Arm II of same; f, sucker from 10th row, arm II, *Del* 63-4 Sta. 7, ML 38.6 mm; g, buccal view of same; h, funnel organ.—i-m, *H. eltaninae*, n. sp., holotype: i, left arm IV; j, largest club sucker; k, sucker from 14th row, arm II; l, buccal view; m, funnel organ.

from as few as 7-9 confined to the distal margin (holotype) to about 20 teeth around entire margin.

Hectocotylization not noted on mature male paratype.

Tentacles long, to more than twice the mantle length, terminating in expanded club. Swimming *keel* present on aboral surface of narrow dactylus portion, longitudinal *cleft* not apparent on manus. Left tentacle of holotype with following *carpal arrangement* from distalmost point from club: 1 p, 2 ss, 2 pp, 2 ss, 2 pp, in single almost median alignment; then, proximal to club, crossing diagonally to the dorsal margin, 2 ss, 2 pp, then 1 s, 1 p, 1 s, 1 p, and at base of manus an enlarged carpal sucker, followed by 1 p, 1 s, 1 p, 1 s, along proximal dorsal margin of manus. Above arrangement more or less typical for species, occasional carpal element may be lacking.

Suckers on manus in five to six rows; third through sixth sucker of median row enlarged three to four times size of other suckers. Largest sucker of holotype with about 52 low, blunt, triangular teeth around entire margin (number varied from about 36-54 in paratypes). Suckers on dactylus small, uniformly decreasing in size. Well-developed *protective membrane* present on each margin of manus, decreasing on dactylus.

Intermixed large and small *photophores* on entire ventral surface of mantle. Large organs in approximately six to seven diagonal rows. Photophores on ventral surface of head in diagonal rows, except for complete circlet of 17 large and one small photophore around right margin of eyelid, and 10 to 12 small photophores in complete circlet around lateral and posterior margins of left eyelid in addition to arc of large organs over anterior margin. Photophores on dorsal surface of mantle and head reduced in size and number. Arms IV with three rows of large photophores basally, no dorsal marginal row of small organs. Dorsalmost row of large photophores with but two to three organs; median row extending to tip, with ventralmost row terminating just short of tip. Base of arms I, II, and III with three longitudinal rows of photophores of decreasing size ventral to dorsal.

Except for point of rostrum, lower *beak* of 57.3-mm-ML ♂ paratype only very lightly pigmented and chitinized. Lateral wall without median ridge.

Male genitalia single, on left side. Mature *spermatophores* (present only in 66.0-mm-ML ♂ paratype) 4.52 to 4.76 mm long (SpLI 0.069-0.072), slender with long cement body (CBI 68.0-67.3). Ejaculatory apparatus occupying oral quarter of spermatophore, with single loop; aboral portion at juncture with cement body swollen but without connective complex. Terminal sperm mass short (SMI 4.2-3.54).

Gladius from above paratype delicate, very lightly pigmented. Vane long (GVLI 75.6; GVWI 22.6); anterior shoulders long and tapering.

Type.—United States National Museum, USNM 576164.

Type-Locality.—Antarctic Ocean, east of Drake Passage, 55°25'S, 58°51' W, 1812-2145 meters.

Discussion.—This species is very close to *H. reversa* (Verrill) and, in fact, during the early study of the material it was considered to be perhaps a subspecies of *reversa*. However, when mature spermatophores became available, they differed structurally so completely from those of *reversa* that no doubt remained that this group of specimens represented a distinct and separate species.

In addition to the distinctive spermatophores, the two species can be readily distinguished by the pattern of photophores on the fourth arms. In *reversa*, there are four longitudinal rows—three rows of large photophores and a dorsal marginal row of small photophores; in *eltaninae*, there are but three rows, all containing large photophores, with the dorsalmost row containing but two or three organs. Even when the marginal row of small photophores has been destroyed in *reversa*, which is often the case, the two are distinguishable by the fact that *reversa* has five to eight organs in the dorsalmost row of large photophores, rather than the two or three in *eltaninae*. *H. eltaninae* can be distinguished from the remaining members of the family by the above characters together with the occurrence of photophores of intermixed sizes on the ventral surface of the mantle, the lack of development of the inner web, and the lack of enlarged terminal photophores on arms I-III.

Increased size of the individual is accompanied by a proportionally narrower mantle and smaller fins.

Remarks.—This species is named for the research vessel USNS ELTANIN. Present work aboard this vessel in the Antarctic and subantarctic is greatly contributing to our knowledge of this area.

A color note on living specimens of *eltaninae* was made in the unpublished "Report on USNS ELTANIN Cruise 23" submitted by E. S. McSweeney, Jr., graduate student of the Institute of Marine and Atmospheric Sciences following his participation in that cruise: "These are striking creatures with blue and reddish-purple photophores studding the mantle, head and arms."

Distribution.—To date, specimens of *H. eltaninae* have been taken only in the subantarctic regions of the South Atlantic and South Pacific oceans from about 58°-175°W and 43°-65°S, all from north of the Antarctic Convergence. This species is the commonest histioteuthid in the collections from these waters. This distributional pattern is an obvious reflection of the restricted collecting in these southern oceans; *eltaninae* will probably be found throughout much of the remainder of the subantarctic region and will be most abundant in proximity to land or oceanic ridges. An interesting reference in this regard was made by McSweeney (*op. cit.*): "Most

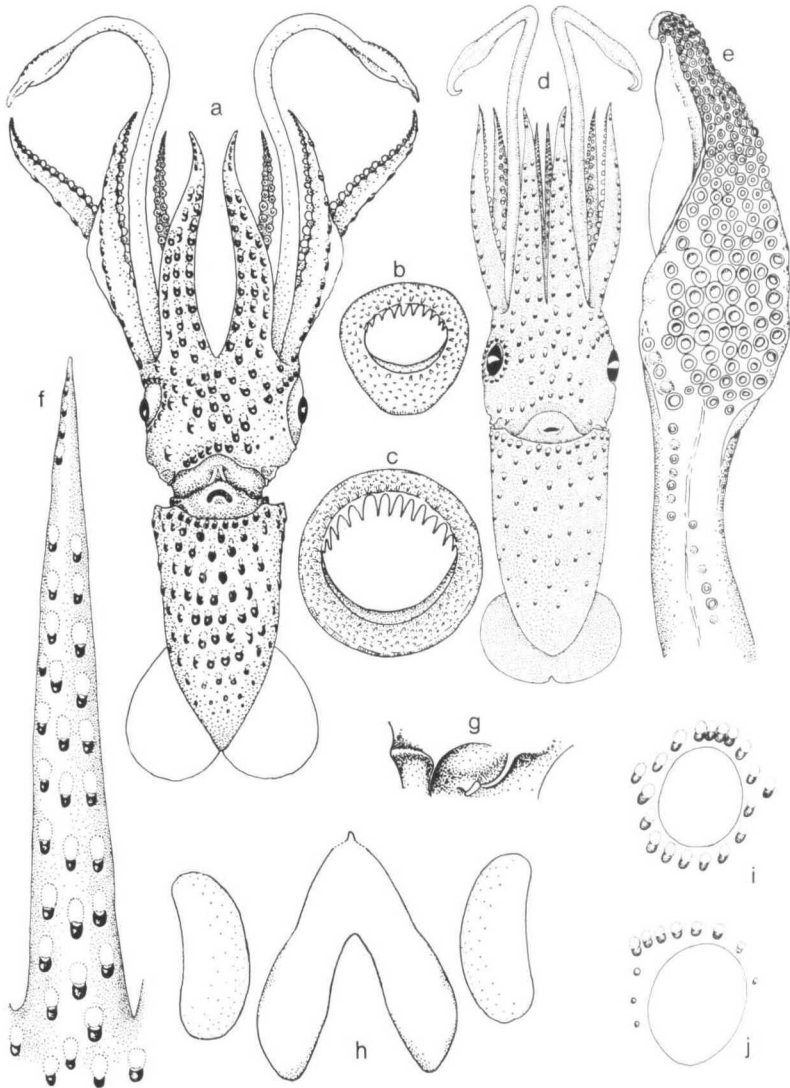


FIGURE 15. *Histioteuthis celetaria celetaria* (G. Voss, 1960): a, ventral view, holotype; b, club sucker, ventral row, holotype; c, largest tentacular sucker, holotype; d, ventral view, MMF 17029, ML 10.3 mm; e, left tentacular club, holotype; f, right arm IV, holotype; g, lateral nuchal view, holotype; h, funnel organ, holotype; i, right eyelid, holotype; j, left eyelid, holotype.

noticeable was the appearance of histioteuthid squid (*H. eltaninae* predominated in the hauls referred to) in the samples approaching the Pacific-Antarctic Ridge. There was a marked concentration of these squids in this region while only occasional specimens were taken from further west."

This species was noticeably absent in the collections of ELTANIN Cruise 26 in the Tasman Sea. Possibly the higher temperature at the preferred depths in this area is the restricting factor.

Specimens were collected by nets fishing to maximum depths of 92 to 2890 meters. Analysis of data showed the greatest concentration of this species to be between about 300-2000 meters.

Histioteuthis celetaria celetaria (G. Voss, 1960)

Figs. 15, 16

Calliteuthis celetaria G. Voss, 1960: 424, figs. 73 a-h.

Calliteuthis celetaria celetaria G. Voss, 1962: 174.—Clarke, M. R., 1966: 197.

Material Examined.—HOLOTYPE: 1 ♀, ML 39.0 mm, CNHM Bermuda Haul 37, 32°10'N, 64°45'W, 5 Aug. 1948, 730-820 meters, CNHM 78308.

OTHER MATERIAL: 1 sex ?, ML 10.3 mm, MMF 17029, Câmara de Lobos, Madeira, 4 April 1960, from stomach of *Alepisaurus ferox*.

Description.—Mantle conical, moderately elongate, walls thick. Sides of anterior half almost parallel; posterior half tapering to blunt point. Dorsally, median anterior margin only slightly produced; ventrally, anterior margin slightly excavated beneath funnel, with sharp lateral angles.

Fins large, slightly longer than half of mantle length; roughly semicircular in outline; in larger specimen, greatest width in posterior half; posterior margin overreaches posterior tip of mantle; median notch present.

Funnel strong with two dorsal supports. *Funnel-mantle locking apparatus* typically histioteuthid with mantle member crescent shaped, heavier posteriorly; funnel cartilage with deep median groove. *Funnel organ* unsculptured; dorsal member inverted V-shaped with long arms and small apical papilla; ventral pads long, slightly kidney-shaped ovals. Large semicircular valve present.

Head large, approximately same width or slightly wider than mantle; typically asymmetrical, with left eye about twice size of right and having correspondingly larger eyelid opening. *Sinus* in anterior margin of both eyelids. Two strong *nuchal folds* on each side of head; dorsal fold slightly curved; ventral fold, or *olfactory crest*, sharply curved dorsally, terminating posteriorly in *olfactory organ*.

Buccal membrane seven-membered with support attachments as follows: first or middorsal support bifurcate to dorsal sides of arms I; second sup-

ports to dorsal side of II; third supports to ventral side of III; fourth supports to dorsal side of IV. *Outer web* not developed; *inner web* vestigial.

Arms approximately equal to length of mantle, stout basally, tapering distally to delicate tips; arms II and III longest, approximately coequal; arm I usually slightly longer than IV; resultant arm formula $2 = 3.1.4$. *Swimming keel* on III originates near base of arm, broad at midarm, then reduced to ridge extending to distal tip. Distal third of arms I and II with low median *keels*.

Arm suckers biserial, relatively large and approximately coequal on basal three-quarters of arm, then decreasing in size to minute suckers at tip. *Horny rings* of large suckers smooth except for occasional sucker on IV; small distal suckers with small teeth on distal border. Suckers on IV about one-third to one-half size of suckers on other arms.

No males available to determine presence or absence of *hectocotylization*.

Tentacles long, terminating in expanded clubs. Orally, *club* with protective membrane on each side; aborally, distal half of club with median *swimming keel*, proximal half without longitudinal *cleft*.

Carpal adhesive apparatus on oral surface of tentacular stalk extending about one club length proximal to club. Following described arrangement from either tentacle, its mirror image on opposite one. Uniserial arrangement commencing at distalmost point from club with single sucker (1 s) near midline, then 2 pads (2 pp), 2 ss, 2 pp, then 2 ss and ?2 pp diagonally set from ventral to dorsal margin, followed by alternating 1 s, 1 p, 1 s, 1 p, 1 s, a short gap, then along dorsal margin of manus a somewhat larger sucker (1 s), followed by 1 p, 1 s, 1 p, 1 s.

In two small individuals available, *suckers* of manus approximately coequal in size, set in six to eight longitudinal rows (rather than "about 10 rows" in original description), decreasing to five and four on dactylus. *Horny rings* of median suckers of manus with about 12-13 sharp triangular teeth on distal margin, proximal margin smooth. Denticulate collar of suckers on proximal portion of manus, principally of first and second ventral rows, distinctly broadened on ventral margin into plate, giving suckers roughly triangular appearance.

With exception of anterior marginal row, *photophores* on ventral surface of mantle uniformly large on anterior two-thirds, abruptly decreasing in size on posterior third; set in approximately six diagonal rows, moderately widely spaced; approximately nine organs in diagonal row commencing at lateral angle. Dorsal surface of mantle with numerous small photophores over most of surface.

Dorsal surface of head with scattered small photophores, few large ones concentrated in vicinity of dorsoanterior margin of eyelids, principally right eyelid. Seventeen large photophores in circlet around right eye; left eye with arc of seven large photophores over anterior margin with three small

TABLE 4
MANTLE MEASUREMENTS (IN MM) AND INDICES OF
Histioteuthis celetaria celetaria (G. Voss, 1960)

	Holotype CNHM 78308 ♀	MMF 17029 —
ML	39.0	10.3
MLI	40.5	37.6
MWI	51.0	58.3
HLI	49.5	53.4
HWI	56.4	56.6
FLI	53.8	50.5
FWI	71.8	68.0
AI I	89.0	80.5
II	92.4	84.5
III	92.8	87.5
IV	84.0	79.6
TLI	205.0	155.4
CLI	26.1	37.9
M+I	—	15.5

organs continuing around ventral margin, single small photophore on anterodorsal margin. Remaining photophores on ventral surface of head, except for those in posterior marginal row, set in diagonal rows. Two spots devoid of photophores present, suggesting "windows," one on either side of median line.

Arms IV with three longitudinal rows of large photophores; ventral row of nine to ten organs extends up about three-fourths length of arm; dorsal row of seven organs extends up about half length of arm; median row of nine to ten organs followed by definite space, then five additional normal organs (in holotype), which regularly diminish in size, extend to tip. Juvenile of 10.3 mm ML with only two organs of latter group developed. Arms I, II, and III with ventral row of large photophores extending to distal end, with similar break in row prior to terminal group of normal organs; less developed dorsal row of small photophores present.

No males available for description of *male genitalia* and *spermatophores*.

Because of small size and uniqueness of material, the *gladius*, *beaks*, and *radula* not extracted.

Type.—Chicago Natural History Museum, CNHM 78308.

Type-Locality.—Western North Atlantic, off Bermuda, 32°10'N, 64°45'W, 730-820 meters.

Discussion.—Since the original description of this species (G. Voss, 1960) from a unique specimen (39.0-mm-ML ♀ from off Bermuda) an additional

specimen of 10.3 mm ML has been acquired. This latter individual was from the stomach of an *Alepisaurus ferox* taken off the Madeira Islands. Though the new specimen is quite small, it is in excellent condition and was the source of additional information, thereby making possible the preceding expanded description.

In the original description of the photophore pattern of arms IV, the row of large photophores approaching the distal tip of the arm was noted to have a distinct break in it near the tip, which defined a definite terminal group of photophores. The tips of the other arms were in too poor a condition to render details. However, examination of the new specimen reveals that there is a similar break in the ventral row of large photophores on arms I, II, and III, thereby defining a definite terminal group. These terminal photophores are normal in size and not differentiated except by their separation. It is possible that in much larger specimens some size differentiation might occur. The number of photophores in these terminal groups increases with the size of the animal. The final number borne by an adult is not known at present.

Another feature, not originally described but apparent from the original illustration, was verified from the new specimen; that is, the presence on the ventral surface of the head of an area to either side of the midline which is devoid of photophores, thereby suggesting "windows." The underlying eyeballs were examined for possible photophores, but none were found.

The tentacular sucker rings of the 10.3-mm-ML juvenile were in too poor a condition to render details of dentition. The arrangement of the suckers on the manus had a mosaic-like appearance. At this size, the unusual platelike development of the denticulate collar is not conspicuous.

As found in other species, growth may be accompanied by a change in certain bodily proportions. A greater differentiation in size of the median suckers on the manus of the club might also occur with increased size of the animal.

The most striking characters separating *Histioteuthis celetaria celetaria* from the other histioteuthids are the shelflike development of the denticulate collar of certain of the suckers of the manus, the terminal groups of normal photophores on the tips of all of the arms, the presence of the clear window-like areas in the photophore pattern on the ventral surface of the head, and the two strong nuchal folds. Since the dentition of the suckers on both arms and tentacles is found to be somewhat variable in other species, I would hesitate at this time, on the basis of the available material, to use the dentition as a distinctive specific character.

A discussion of the distinguishing characters between *H. celetaria celetaria* and the next described subspecies *H. celetaria pacifica* is deferred until the discussion of the latter subspecies.

Distribution.—At present, *H. celetaria celetaria* is known from but two records, one from the western North Atlantic off Bermuda, and one from the eastern North Atlantic off the Madeira Islands, with depths of capture of 730 to 820 meters.

Histioteuthis celetaria pacifica (G. Voss, 1962)

Figs. 4, h-i; 5, d; 7, e; 16; 17

Calliteuthis celetaria pacifica G. Voss, 1962: 174; 1963: 199, fig. 26.—Clarke, M. R., 1966: 197.

Material Examined.—HOLOTYPE: 1 ♀, ML 74.0 mm, ALBATROSS Sta. D5564, Dammi Island, between Jolo and Tawi Tawi, Philippines, 21 Sept. 1909, 432 meters, USNM 575453.

PARATYPES: 1 ♂, ML 58.0 mm, ALBATROSS Sta. D5221, San Andreas Island, Philippines, between Marinduque and Luzon, 24 April 1908, 354 meters, UMML (mistakenly labeled in Voss [1962] as ♀).—2 ♀♀, ML 52.0-33.0 mm, ALBATROSS Sta. D5589, Mabul Island, Borneo, 29 Sept. 1901, 494 meters, USNM 575457.—1 ♀, ML 51.0 mm, ALBATROSS Sta. D5118, Sombrero Island, Philippines, 13°48'45"N, 120°41'51"E, 21 Jan. 1908, 292 meters, USNM 575454.—1 ♀, ML 28.0 mm, ALBATROSS Sta. D5268, Matacot Point, Verde Island Passage, Philippines, 8 June 1908, 310 meters, USNM 575455.

OTHER MATERIAL: 1 ♀, 1 ♂, ML 88.0, 74.0 mm, GALATHEA Exped. 1950-52, Sta. 202, 25°20'S, 35°17'E, off Natal, 21 Feb. 1951, ZMUC.

Description.—Mantle conical, moderately elongate; sides of anterior third nearly parallel, sides of posterior two-thirds tapering to blunt posterior tip. Dorsally, anterior margin slightly produced medially; ventrally, anterior margin slightly excavated beneath funnel, lateral angles blunt. Wall thick.

Fins large, slightly longer than half the mantle length; wide, about 70 per cent of mantle length. Transversely oval in outline; posterior border usually slightly overreaches tip of mantle, with shallow median notch.

Funnel strong, with heavy double bridle. Funnel-mantle locking apparatus strong; crescent-shaped ridge on mantle heavier posteriorly, funnel cartilage broad with deep median groove. Dorsal member of funnel organ inverted V-shaped pad with apical papilla and long arms, unsculptured; two long oval ventral pads. Valve large, semicircular.

Head large, as wide or slightly wider than mantle width, sharply angled at neck; asymmetrical, with left eye about twice as large as right. Sinus in anterior margin on both eyelids. Two strong nuchal folds on either side of head; dorsal fold slightly curved dorsally; ventral fold, or olfactory crest, strongly curved dorsally, terminating in olfactory organ.

Buccal membrane with seven lappets and seven supports. Attachments as follows: middorsal or first support bifurcate to dorsal sides of arms I;

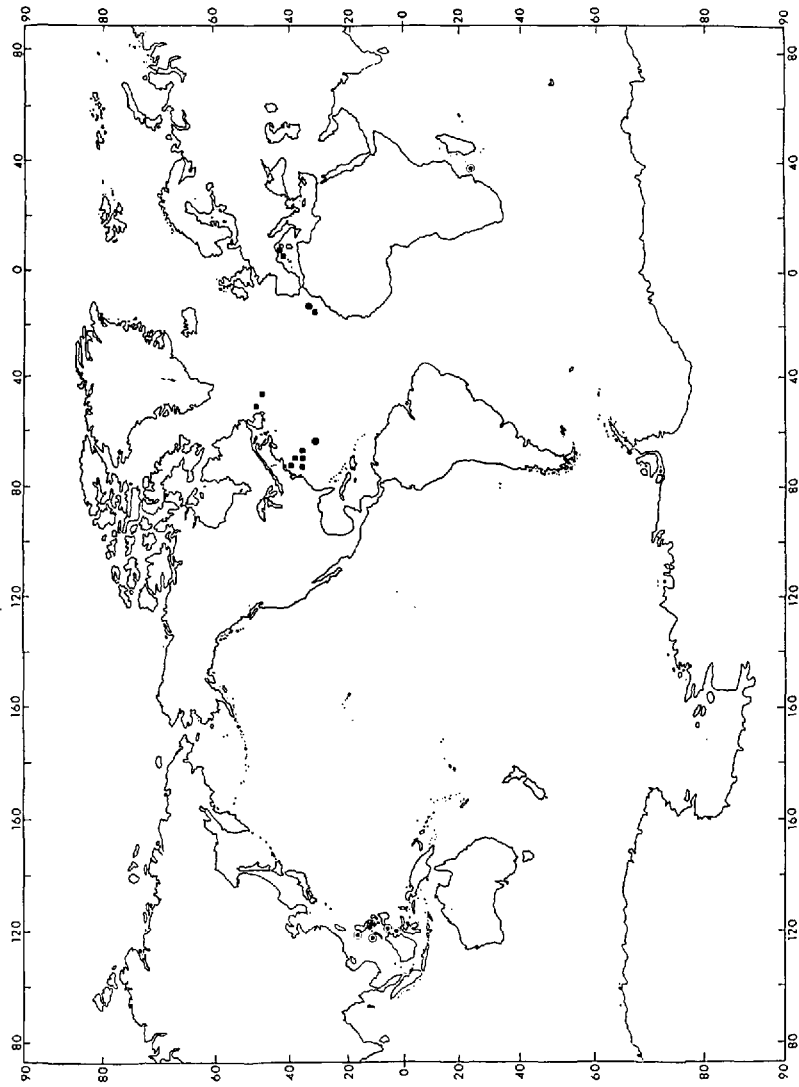


FIGURE 16. Distribution of confirmed, identified specimens. ● = *Histioteuthis celestaria celestaria* (G. Voss); ○ = *H. celestaria pacifica* (G. Voss); ■ = *H. elongata* (Voss & Voss).

second supports to dorsal sides of II; third supports to ventral sides of III; fourth supports to dorsal sides of IV. *Inner web* vestigial; *outer web* not developed.

Arms roughly equal to length of mantle. Arms II and III the longest, approximately coequal; arms I usually longer than IV; approximate arm formula $2 = 3.1.4$. Arms I and II with low, median *keels* on terminal third. *Swimming keel* on III originates near base of arm, reduces to ridge at about midarm, continues as such to tip. Orally, low *protective membrane* on either margin of arms.

Arm suckers biserial, approximately uniform in size on proximal two-thirds of arm; on distal third, a rather abrupt reduction in size to minuteness at tip. Suckers on IV, about one-third smaller than on other arms. *Horny rings* of suckers smooth, except near tips of all arms.

No sign of *hectocotylization* on dorsal arms of mature male.

Tentacles long, terminating in expanded *club*. Aborally, posterior half of club with median *swimming keel*, anterior half without longitudinal *cleft*. Orally, low protective membrane along either margin.

Suckers of manus in about six to seven rows; distinctly larger than those on attenuate dactylus. Suckers of three or four median rows larger, but not excessively, than those of two ventral and of dorsal marginal rows. Large median suckers with about 28-32 pointed teeth on entire margin, usually smaller on proximal margin and heavier, longer, and curved inward on distal margin. Suckers of two ventral rows and a few proximal suckers of median row with denticulate collar on ventral side asymmetrically developed into a shelf or plate.

On oral surface of tentacular stalk, *carpal adhesive apparatus* extends to about one to one and a half length of club proximal to manus; commencing at this point, single small sucker (1 s) near midline, followed by two widely set pads (2 pp), 2 ss, 2 pp in a single row, then crossing diagonally 2 ss, 2 pp, and continuing up dorsal margin of stalk 1 s, 1 p, 1 s, 1 p, 1 s, space, then somewhat enlarged suckers (1 s) at base of manus followed by 1 p, 1 s, 1 p, 1 s, 1 p along dorsal margin of manus (occasional element sometimes lacking). Above arrangement on either tentacle, mirror image on opposite.

Numerous large *photophores* on ventral surface of mantle regularly set in about seven diagonal rows extending to near posterior tip of body. Posterior third of mantle with additional interspersed small photophores. Photophores on dorsal surface of mantle reduced in size and number, with both large and small organs intermixed.

Dorsal surface of head with few widely set small photophores; a few large ones in vicinity of dorsoanterior margin of right eyelid. Numerous large photophores on ventral surface of head set in diagonal rows, with exception of circlet of 17 large photophores around margin of right eyelid

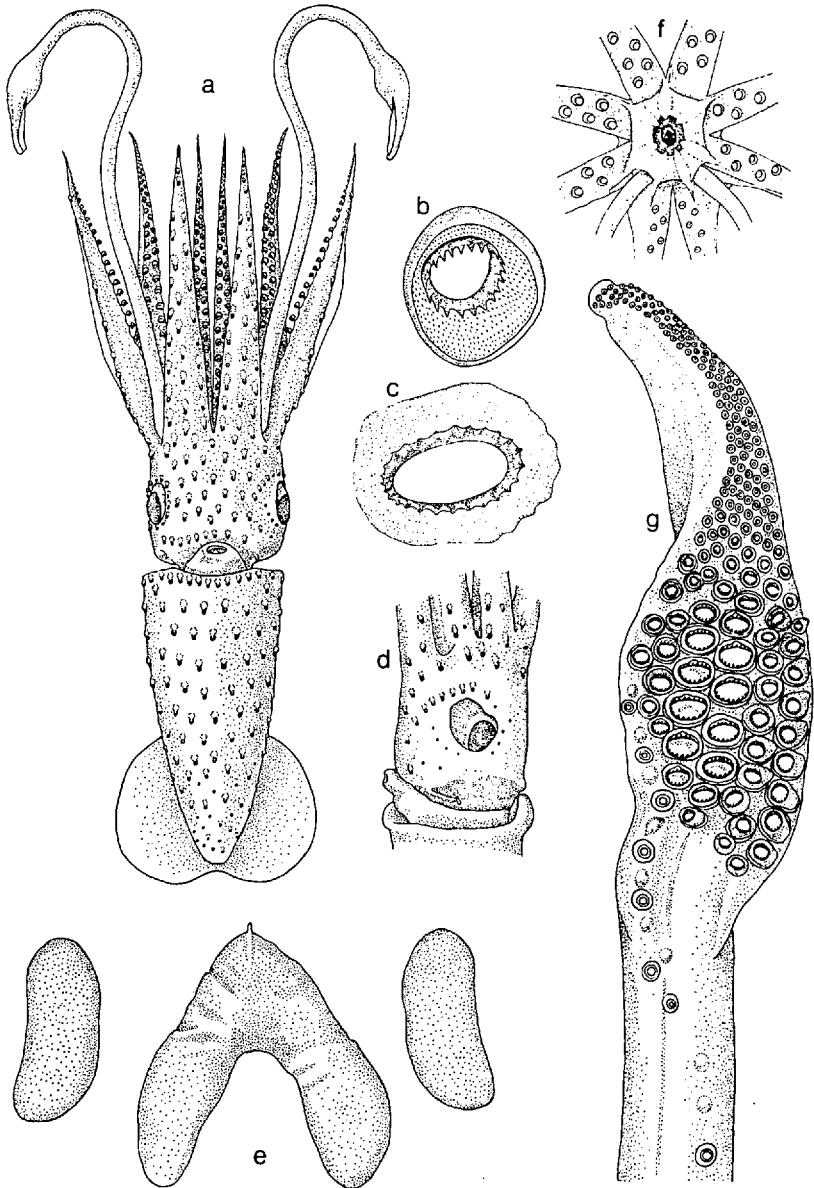


FIGURE 17. *Histioteuthis celetaria pacifica* (G. Voss, 1962), *G* 202, ML 74.0 mm: a, ventral view; b, club sucker, ventral row; c, largest club sucker; d, left lateral view of head; e, funnel organ; f, buccal view; g, left tentacular club.

and seven large photophores in arc over anterior margin of left eyelid with eight or nine small organs in broken series partially encircling remaining portion of margin of the lid. No spots conspicuously free of photophores that might suggest "windows." Photophores along posterior margin of head closely set in marginal row.

Two rows of photophores on arms I, II, and III; ventral row of large organs extending to tip of shorter dorsal row of small organs. Arm IV with three rows of large organs with only median row extending to tip. Dorsal row of about five to seven photophores terminates at slightly less than two-thirds length of arm. Ventral row terminates just short of tip. Presence or absence of break in row of photophores extending to tip, thereby defining separate terminal group of photophores on arms, uncertain at present due to poor condition of tips of arm on all available specimens except for arms IV of *GALATHEA* specimen (74 mm). In this latter specimen there are strong indications of a terminal group of at least four photophores.

Male with single set of *genitalia*, on left side. Male of 58.0 mm ML with *spermatophores*. Spermatophores in poor condition (illustration result of some reconstruction), SpL approximately 2 mm; appear to have ejaculatory apparatus with single large loop. Cement body with oral connective complex with high thin collar and deep cavity. Ejaculatory apparatus and cement body of approximately coequal length, about 35 to 40 per cent of spermatophore; sperm mass, 21 to 25 per cent.

Gladius delicate, very lightly pigmented, except along margins of rhachis. Vane long (GVLI 65), moderately broad (GVWI 23.5), in gladius of 63.0 mm, with slightly thickened and more heavily pigmented posteriorly tapering lateral margins. Rhachis ends posteriorly in small coil.

Radula with weak marginal plates. Rhachidian stout; laterals of increasing size.

Lower *beak* with strong median ridge bisecting lateral wall.

Type.—United States National Museum, USNM 575453.

Type-Locality.—Dammi Island, between Jolo and Tawi Tawi, Philippines, 432 meters.

Discussion.—*Histioteuthis celestaria pacifica* was first described by G. Voss in 1962 from six specimens collected by the ALBATROSS, 1907-1909, in the vicinity of the Philippine Islands. In 1963, the description was expanded in his more comprehensive work, "Cephalopods of the Philippine Islands." The specimens were noted to be similar to the Atlantic *H. celestaria*, yet they varied so consistently in certain small characters, that they were considered as representing a separate subspecies.

Since that time, one additional specimen of *c. celestaria* from the opposite side of the Atlantic, and two new specimens of *c. pacifica* from the Indian

TABLE 5
MANTLE MEASUREMENTS (IN MM) AND INDICES OF
Histioteuthis celetaria pacifica (G. Voss, 1962)

	G 202 ♀	Holotype USNM 575453 ♀	Paratypes				
			UMML ♂	USNM 575457 ♀	USNM 575454 ♀	USNM 575457 ♀	USNM 575455 ♀
ML	88.0	74.0	58.0	52.0	51.0	33.0	28.0
MWI	41.4	43.3	43.1	38.5	44.2	48.5	50.0
HLI	—	35.1	44.9	50.0	41.2	53.0	46.5
HWI	43.2	37.9	41.4	40.4	39.3	45.5	57.2
FLI	42.6	55.4	51.7	55.8	59.0	56.1	57.2
FWI	62.5	73.0	67.3	77.0	77.5	69.7	75.0
AI I	88.7	104.0	103.0	112.0	114.0	91.0	86.0
II	107.0	111.0	112.0	121.0	129.0	109.0	96.5
III	96.5	111.0	108.0	123.0	121.0	106.0	96.5
IV	78.5	105.0	84.5	102.0	106.0	100.0	82.0
TLI	—	223.0	176.0	188.0	212.0	—	171.0
CLI	—	29.7	29.3	38.0	16.6	—	26.8
M+I	—	0	3.0	2.0	1.0	3.0	2.5

Ocean off the southeast coast of Africa, similarly far removed from the type-locality, have been studied. Both lots were identical with their respective types, and neither lot showed significant variation. This new material confirms the fact that we are working with two taxonomically distinct groups. I concur with G. Voss that, with our present knowledge, the differences between the two are of subspecific value.

H. c. pacifica may be distinguished from *H. c. celetaria* in that it lacks the window-like areas devoid of photophores on the ventral surface of the head; it has a larger number of small photophores in the pattern around the margin of the left eyelid, i.e., eight or nine rather than about four, as in *c. celetaria*. Of possible importance is the presence of teeth around the entire margin of the tentacular suckers of the manus rather than only on the distal margin. Since this latter character is based on only a single specimen with dentition of the tentacular suckers intact in the case of *c. celetaria*, its value as a distinguishing character must await additional material.

Histioteuthis celetaria pacifica may be distinguished from the remaining members of the family by the shelflike development of the denticulate collar of certain of the tentacular suckers and the two strong nuchal folds on either side of the head.

Distribution.—*H. celetaria pacifica* is presently known from the North Pacific in the vicinity of the Philippine Islands and Borneo and from the Indian Ocean off the southeast coast of Africa, in depths ranging from

292 to 494 meters. It will probably be found to be widespread throughout the Indo-Pacific region.

Histioteuthis corona corona (Voss & Voss, 1962)

Figs. 4, f, g; 6, a; 7, f; 18; 19

Calliteuthis reversa G. Voss, 1956: 139.

Calliteuthis corona Voss & Voss, 1962: 191, figs. 5 a-f, 6 b-d.—Taki, 1964: 291.

Material Examined.—HOLOTYPE: 1 ♀, ML 46.0 mm, OREGON Sta. 384, 29°10'N, 88°00'W, 21 June 1951, 521 meters, USNM 576160.

PARATYPES: 1 ♀, ML 156.0 mm, OREGON Sta. 1914, 13°06'N, 82°13'W, 12 Sept. 1957, 640 meters.—1 ♀, ML 96.0 mm, OREGON Sta. 1018, 24°16'N, 83°22'W, 16 April 1954, 685 meters.—1 ♀, 38.0 mm, OREGON Sta. 639, 29°12.4'N, 88°20.6'W, 19 Sept. 1952, 365 meters.—1 ♀, ML 30.0 mm, ATLANTIS Sta. 22, 27°09'N, 86°43'W, 12 April 1937, mw 2000, YPM 12439.—1 ♀, ML 20.0 mm, OREGON Sta. 2370, 22°10'N, 91°20'W, 5 Dec. 1958, 59 meters.

OTHER MATERIAL: 1 ♀, 1 ♂, ML 136.0-54.5 mm, OREGON Sta. 3653, 29°12'N, 87°52'W, 25 July 1962, 512-548 meters.—1 ♂, ML 110.8 mm, OREGON Sta. 4300, 7°44'N, 54°19'W, 23 March 1963, 549 meters.—1 ♂, ML approx. 75 mm, Funchal Fish Market, Madeira Island, from fish stomach, MMF 5583.—1 ♂, ML 54.0 mm, OREGON Sta. 4882, 10°16.2'N, 75°54.4'W, 25 May 1964, 549 meters.—1 ♀, ML 50.0 mm, GALATHEA Sta. 235, 4°47'S, 46°19'E, 2 March 1951, mw 7440.—1 ♂, 1 ♀, ML 42.0-40.2 + mm, OREGON Sta. 3296, 28°36'N, 89°48'W, 21 Aug. 1961, 446-950 meters, UMML 31.390.—2 ♀♀, 3 sex ?, ML 31.2-12.3 mm, OREGON Sta. 3254, 29°00'N, 88°02'W, 27 April 1961, 247 meters, UMML 31.383.—2 ♀♀, ML 32.6-31.0 mm, OREGON Sta. 2507, 29°05'N, 88°09'W, 20 May 1959, 823 meters.—1 ♀, ML 32.0 mm, DANA Sta. 3980 VI, 23°26'S, 3°56'E, 17 Feb. 1930, mw 6000.—1 sex ?, ML approx. 28 mm, SILVER BAY Sta. 1196, 24°11'N, 83°21.5'W, 8 June 1959, 730 meters.—1 ♀, ML 27.7 mm, A. BRUUN Cr. 7, Sta. 363 K, 23°34'S, 43°25'E, 8 May 1964, 1080-1280 meters, Webb trawl.—1 ♀, ML 20.5 mm, DANA Sta. 4147 VI, 36°39'N, 8°06'W, 10 June 1930, mw 1000.—1 sex ?, ML 16.8 mm, DANA Sta. 4019 IV, 33°08'N, 10°22'W, 30 March 1930, mw 2000.—1 sex ?, ML 16.5 mm, GERDA Sta. 88, 25°02'N, 79°48'W, 8 March 1963, mw 1500.—1 ♂, ML 15.0 mm, PILLSBURY Sta. 303, 2°55'N, 4°48'E, 25 May 1965, 800-900 meters.—1 sex ?, ML 13.5 mm, DANA Sta. 1171 IV, 8°19'N, 44°35'W, 13 Nov. 1921, mw 300.—1 sex ?, ML 13.0 mm, DANA Sta. 1342 IV, 34°00'N, 70°01'W, 15 May 1922, mw 2000.—2 sex ?, ML 11.2-8.5 mm, DANA Sta. 4017 IV, 29°11'N, 14°14'W, 27 March 1930, mw 2000.

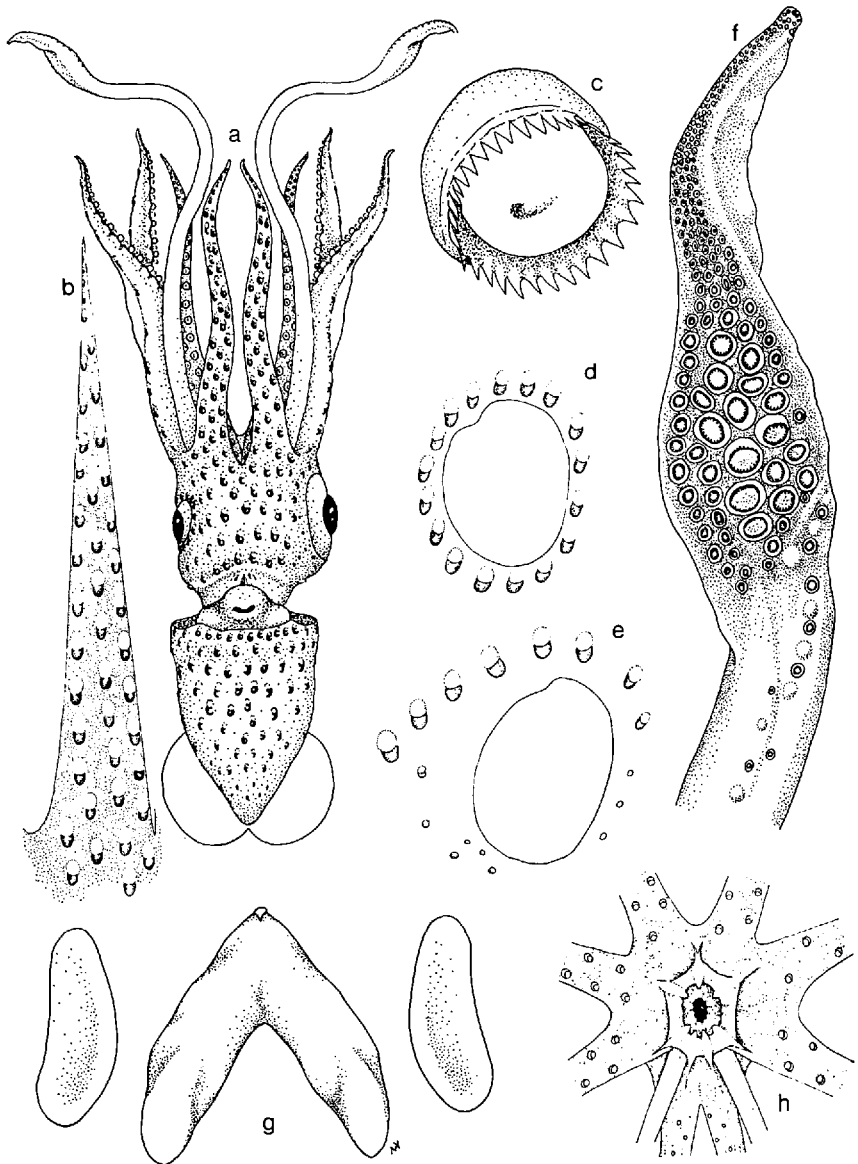


FIGURE 18. *Histioteuthis corona corona* (Voss & Voss, 1962): a, ventral view, *O* 2507, ML 32.6 mm; b, right arm IV, holotype; c, largest tentacular sucker of paratype, *O* 1018, ML 96.0 mm; d, right eyelid of same; e, left eyelid of same; f, right tentacular club of same; g, funnel organ, *O* 2507; h, buccal view, *O* 3653, ML 54.5 mm.

Description.—*Mantle* conical, sides tapering to blunt point posteriorly; walls relatively thick and firm. Mantle width about 52-70 per cent of ML in size range of 16.8-96.0 mm ML; larger individuals tending to have slimmer mantles (42.6-47.8 per cent of ML in three individuals measuring 110.8-156.0 mm ML). Anterodorsal margin slightly produced in midline; anteroventral margin very slightly emarginated beneath funnel.

Fins transversely oval, length about 50 per cent of ML, or under; width approximately 57-82 per cent of ML. Lobes united posteriorly with central notch; may extend beyond posterior tip of mantle in small individuals.

Funnel stout with two dorsal supports. *Funnel-mantle locking apparatus* typically histioteuthid, funnel cartilage broad with deep central groove. *Funnel organ* consisting of two long, oval, ventral pads, broadest posteriorly; inverted V-shaped dorsal pad with moderately long arms and anterior papilla. Surface of dorsal pad distinctly swollen; in long-preserved specimens often appearing deflated. *Valve* semicircular.

Head typically histioteuthid, large, slightly wider than mantle. Left eye more than twice size of right; sinus in dorsal anterior margin of both eyelids. Two *nuchal folds* on each side of head (not always apparent in specimens in poor condition); dorsalmost fold almost straight, curving slightly dorsally; ventral fold strongly curved dorsally, terminating posteriorly in fleshy papilla-like *olfactory organ*.

Buccal membrane seven-membered; seven support attachments as follows: first support bifurcate to dorsal sides of arms I; second supports to dorsal side of II, third supports to ventral side of III; fourth supports to dorsal of IV. *Inner web* connecting first three pairs of arms heavily pigmented, moderately deep, depth range from about 11-25 per cent of longest arm; *outer web* not developed.

Arms approximately one to two times mantle length, relatively heavy basally, tapering to slender tips; arm order usually 2.3.1.4 or 2 = 3.1.4. *Swimming keel* on terminal two-thirds of arm III, at first expanded, then reduced to ridge to tip of arm; arms I and II with keels terminally.

Arm suckers moderate size; those on arm IV small, about one-third to one-half size of those on other arms; those on arms I-III largest on median third; slightly smaller on basal third, diminishing rapidly in size to minuteness on distal third. *Horny rings* of suckers on arms I-III usually smooth except near arm tips where rings usually have numerous low teeth; some basal suckers with few barely distinguishable teeth on distal margin. Sucker rings on arm IV with numerous low square teeth on entire or distal margin. Marginal low fleshy *protective membranes* all but disappear beyond basal third of arm. No *hectocotylization* apparent in males.

Tentacles long with expanded *club*. Low *swimming keel* on distal half of aboral surface of club; no longitudinal cleft in proximal half in available specimens. Orally, manus of club with five to six rows of suckers decreas-

ing to four, and three, and sometimes two rows on slender dactylus. Large specimens with five to six pairs of median suckers on manus, starting at about third sucker from base of manus, enlarged one and a half to two times in size; size difference less in smaller specimens. *Horny rings* of suckers on manus with sharp pointed teeth on entire margin. Enlarged suckers with approximately 33-35 teeth, triangular or thin straight-sided. Low *protective membrane* on either side of manus.

Carpal adhesive apparatus uniserial, commencing on dorsal margin approximately one and a half club-lengths proximal to club with widely set 1p, 2 ss, then with decreasing intervening space, 2 pp, 2 ss, 2 pp all in single alignment, then 2 ss, 2 pp and 2 ss diagonally set in double row across stalk to ventral margin. Arrangement continues uniserially with 1 p, 1s, 1 p, 1 s, to base of club, followed by enlarged pad rather centrally set at base of manus, then by two or three suckers alternating singly with one or two pads along ventral margin of manus. Latter group separated from suckers of manus by fleshy ridge.

Photophores on ventral surface of mantle numerous, regularly set in about eight diagonal rows (each consisting of approximately ten photophores) to near posterior tip; no intermixture of size, large on anterior half, progressively smaller in size on posterior half. Photophores on dorsal surface of mantle smaller and fewer in number.

Photophores on ventral surface of head set in diagonal rows, except for series surrounding each eyelid. Seventeen large light organs evenly spaced in circlet around right margin of eyelid; seven to eight large light organs in arc over anterior margin of left eyelid with three small light organs on dorsal margin and four small ones on ventral margin of lid, two smaller additional photophores usually on more immediate postero-ventral margin. Six to seven photophores in posterior marginal row of head. Dorsal surface of head with fewer and generally smaller photophores set in about three widely spaced diagonal rows; several of central organs, prominent round type, lacking well-developed anterior lens.

Arm IV with three longitudinal rows of photophores; dorsal row of eight to ten organs terminating about three-quarters of the way up arm; ventral row terminating shortly thereafter; median row extending to tip. Arms I, II, and III with two longitudinal rows of photophores; dorsal row of small ones and ventral row of large ones with only latter row extending to tip; in some specimens an irregular third longitudinal row of minute photophores present on III and II.

Male genitalia single, on left side. Mature *spermatophores* present only in male of 110.8 mm ML (OREGON Sta. 4300). Spermatophores relatively stubby, 2.42 to 2.76 mm long (SpLI 0.021-0.023), with ejaculatory apparatus and sperm mass of approximate coequal length, each slightly more than one-third the length of spermatophore. Ejaculatory tube flexed

into single large loop occupying greater portion of oral end of spermatophore. Cement body slightly more than half length of ejaculatory apparatus; oral connective complex relatively simple with low fleshy collar around central pedestal and intervening shallow cavity. Granular textured oral half of cement body delineated by constriction from more hyalin aboral half. Sperm mass appears in about five to seven stout coils.

Gladius thin, transparent, deeply concave on ventral surface. Delicate vane long (GVLI 72.8-83.0), and moderately broad (GVWI 20.8-18.8), in pens of 46.0 and 175.3 mm length respectively, lateral margins slightly thickened and pigmented. Lateral margins of rhachis heavily pigmented; typically, rhachis terminating posteriorly in tight coil cupped within concavity of posterior margin of vane.

Lower *beak* with strong median ridge on lateral wall.

Radula of a specimen from Gulf of Mexico illustrated. Teeth definitely heterodont. Rhachidian symmetrical; both first and second laterals, strongly asymmetrical with long, rather narrow bases and rudimentary cusp on outer end of basal plate. Third laterals normal saber-shaped. No marginal plates present.

Type.—United States National Museum, USNM 576160.

Type-Locality.—Gulf of Mexico, 29°10'N, 88°00'W, in 521 meters.

Discussion.—*Histioteuthis corona corona* can be distinguished from the other species of histioteuthids by the following combination of characters: photophore patterns around the eyelids—17 large organs around the right eyelid and a broken circlet of usually seven small organs around the left eyelid; three longitudinal rows of photophores on arm IV; no abnormally enlarged photophores on mantle or tips of arms; uniformly large photophores on the anterior half of the ventral surface of the mantle; moderate inner web between arms I, II, and III; and arms of dorsal funnel organ swollen (in well-preserved specimens, otherwise with deflated appearance but unsculptured).

Again in this species, the armature, or lack of it, on the rings of the suckers on the arms is not a reliable specific character. Though the rings tend to be smooth, with the exception of the first few basal pairs of suckers and those on the tips of the arms, an occasional specimen will have them all toothed.

Though the photophore pattern is specific, a slight variation was noted in the number of photophores around the margin of the eyelids. Of the twenty-four specimens examined, two otherwise normal individuals had sixteen instead of the usual seventeen photophores in the circlet around the right eyelid. In regard to the left eyelid pattern, an occasional specimen lacked the two small photophores on the immediate posteroventral margin

of the lid. None of these variations showed any relationship with geographic distribution.

A considerable degree of variation was noted within the general pattern of the carpal adhesive apparatus described for this species. A detailed study of ten specimens revealed that six had the described arrangement (termed "normal" for convenience) on the right tentacle and club; one had the "normal" arrangement on the left tentacle and club; and three specimens had the "normal" arrangement on the left tentacular stalk, but had the mirror image of the "normal" arrangement on the manus of the club, and where the two half arrangements met at the base of the manus (just proximal to the enlarged pad) there was an additional sucker.

Structurally, the spermatophores in the single lot available were identical to each other except for a slight variation in the number of large convolutions on the sperm mass, which is possibly an artifact of preservation. In regard to the proportions of the three major parts of the spermatophore, individual variation was as high as 18.5 per cent.

One specimen, a female of 96.0 mm ML from the Straits of Florida, displayed an interesting aberrancy on a few of the suckers on the club. Four or five suckers on the distal portion of the manus where it tapers into the dactylus had one to three button-like growths of "collar" tissue on the surface of the outer side of the suckers, isolated from the intact papillated collar which surrounds the sucker ring. Apparently through injury, small bits of "collar" tissue had been separated from the normal position; the collar had repaired itself, and the isolated bits had continued to grow, forming miniature collars complete with elevated margins around a depressed papillated center but lacking the central aperture for the sucker ring.

The most obvious proportional changes accompanying growth in *corona* are a proportional reduction in size of the fins and the width of the mantle.

Remarks.—The subspecific name *corona* is appended to distinguish this form from a newly found Pacific counterpart. A comparison of the two forms is made in the discussion of the new subspecies *berryi*.

Data in Table 6 is from the holotype and certain of the specimens secured since the original description of *corona* by Voss & Voss (1962). Data for the paratypes is not republished here, but may be found in the original study.

Distribution.—Since the original description, additional material has greatly expanded the known distribution of this species. Specimens have been collected in the Gulf of Mexico, the Caribbean Sea, in the North Atlantic south of about 37°N, in the eastern South Atlantic, and in the Indian Ocean off the east coast of Africa.

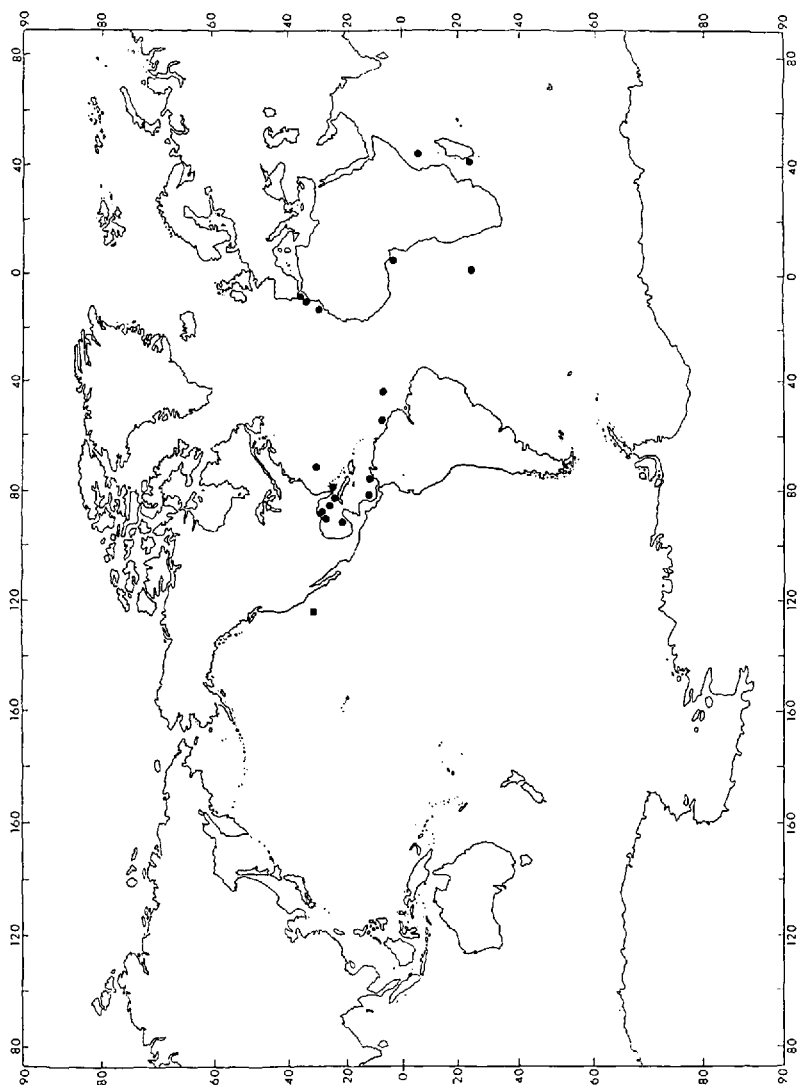


FIGURE 19. Distribution of confirmed, identified specimens. ● = *Histioteuthis corona corona* (Voss & Voss); ■ = *H. corona berryi*, n. subsp.

The captures have been chiefly confined to waters adjacent to land masses, both over the continental shelf and over deeper bottom beyond. Nets successful in catching this species fished at maximum depths of 59 to about 3700 meters. Analysis of data shows the greatest abundance to be at depths of about 200 to 1000 meters.

***Histioteuthis corona berryi*, n. subsp.**

Figs. 19, 20

Material Examined.—HOLOTYPE: 1 ♂, ML 47.4 mm, SIO XIX-2, 29°17'N, 125°41'W, 12 May 1955, mw 750, USNM 576079.

PARATYPE: 1 ♀, ML 36.0 mm, SIO XIX-3, 29°17'N, 125°41'W, 12 May 1955, mw 750, SIO.

Description.—These two specimens taken together in the northeastern Pacific compare well with the preceding subspecies *H. corona corona* in regard to the conical *mantle* of moderate length, size of *fins*, unsculptured but swollen surface of the *funnel organ*, single *male genitalia*, details of the seven-membered *buccal membrane*, moderately developed *inner web*, and lack of dentition on the rings of the *suckers* on arms I, II, and III except for the minute distal suckers.

The most obvious difference between the two above specimens and *c. corona* is in the pattern of photophores on the arms. In *c. berryi*, arms IV bear four longitudinal rows of large photophores; the dorsal marginal row of 9-10 organs extends to almost the midarm (the holotype has a couple of additional small photophores basally); the second dorsal row extends to three-quarters of the arm length; the ventral row terminates shortly thereafter, and only the second ventral row extends to the tip. Arms III have three distinct rows of photophores decreasing in size from the ventral to the dorsal row, with apparently only the ventral row of large organs extending to the tip; arms II and I appear to have the same pattern as on III, but with smaller photophores. In *c. corona*, there are but three rows of large photophores on IV, two on arms I, and usually two on II and III.

As in *c. corona*, there are seventeen large photophores around the margin of the right eyelid; around the margin of the left eyelid, the pattern is the same with the exception of the absence of the two small photophores on the immediate ventral margin of the lid. (They are also missing in the otherwise normal specimen of *c. corona* from the Indian Ocean off Madagascar.) The paratype had an additional small photophore on the dorsal anterior margin.

The 47.4-mm-ML holotype contained no *spermatophores*; no signs of *hectocotylization* were apparent on the first pair of arms.

The right *tentacle* of the holotype was the only one remaining on the

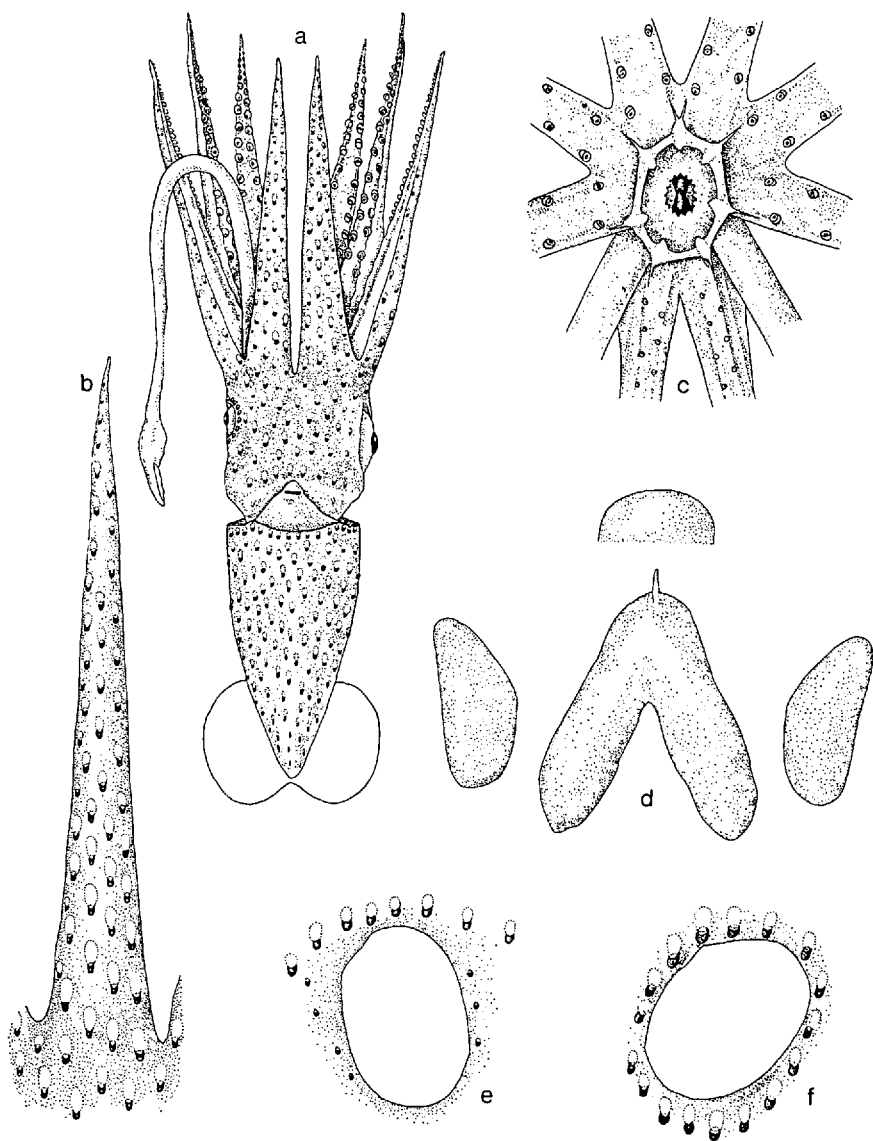


FIGURE 20. *Histioteuthis corona berryi*, n. subsp., holotype, ML 47.4 mm: a, ventral view; b, right arm IV; c, buccal view; d, funnel organ and valve; e, left eyelid; f, right eyelid.

TABLE 7
MANTLE MEASUREMENTS (IN MM) AND INDICES OF
Histioteuthis corona berryi, n. subsp.

	Holotype USNM 576079 ♂	Paratype SIO XIX-3 ♀
ML	47.4	36.0
MLI	35.6	36.8
MWI	49.0	55.3
HLI	50.6	47.2
HWI	57+	63.9
FLI	40.2	43.6
FWI	61.2	65.0
AI I	110.0	97.5
II	118.3	114.0
III	112.0	105.7
IV	98.5	94.5
TLI	199 (approx.)	—
CLI	28.7	—
M+I	6.3	6.9
IWI A	18.2	18.1
B	14.3	14.6
C	14.7	23.4

type-specimens and it was not completely intact. It compared well with that of *c. corona* in all respects except possibly for the *carpal adhesive apparatus*, which is more abbreviated than in *c. corona*, but this could possibly be due to individual variation or the poor condition of the tentacular stalk. From a point on the stalk roughly one club-length proximal to the manus, the arrangement is as follows: uniserial along ventral margin 1 s, 2 pp, 2 ss, 2 pp, then diagonally across the stalk 2 ss, 2 pp; uniserial up dorsal margin of stalk 1 s, 1 p, 1 s, 1 p, followed by 1 s slightly enlarged at the base of the manus; then along dorsal margin of the manus 1 p, 1 s, 1 p, 1 s.

The horny rings in the remaining suckers of the manus were uniformly incised around the entire margin with approximately 28-30 sharp-pointed triangular teeth, somewhat fewer than the 33-55 teeth found to be common in *c. corona*.

Gladius, *beaks*, and *radula* not extracted.

Type.—United States National Museum, USNM 576079.

Type-Locality.—Northeastern Pacific Ocean, 29°17'N, 125°41'W, 750 mw.

Discussion.—The primary difference between *Histioteuthis corona berryi* and *corona corona* is the presence of four longitudinal rows of large photophores on arms IV in *c. berryi*, while there are only three in *c. corona*.

The smaller number of teeth on the rings of the suckers on the manus of the club could be of value, but since this character has been found to be somewhat variable in other species in the family, its value as a distinctive character here must remain in question until additional material of *c. berryi* is available.

I consider the two groups to be sufficiently distinct to warrant separation on a subspecific level.

Remarks.—This subspecies is named for Dr. Stillman Berry of Redlands, California, who has worked a lifetime with cephalopods and whose "home waters" yielded the type material.

Distribution.—Known only from the two type-specimens taken together in the northeastern Pacific, 29°17'N, 125°41'W, at a maximum fishing depth of about 250-300 meters.

Histioteuthis dofleini (Pfeffer, 1912)

Figs. 3, a-c; 5, e, f; 8, a, b; 21-23

Calliteuthis reversa Verrill, Chun, 1906: 744, figs. 2, 4, 5.

Calliteuthis ocellata (Owen), Chun, 1910: 149-170 (in part: only references to *C. ocellata*), text-figs. 22, 23, text-pl. 1, figs. 1, 2, pl. 20, figs. 7, 8, 9. ?*Calliteuthis Hoylei* (Goodrich), Chun, 1910: 170, pl. 18, fig. 1, pl. 19, fig. 6, pl. 20, figs. 1, 2, 5, 10, 12.

?*Stigmatoteuthis Chuni* Pfeffer, 1912: 286.

Stigmatoteuthis Dofleini Pfeffer, 1912: 288.—Sasaki, 1916: 98; ?1920 (incomplete specimen): 197; 1929: 258, text-figs. 126, 127, pl. 22, figs. 1-3.—Dell, 1959: 99.—Akimushkin, 1963: 193, fig. 54.

Calliteuthis Meneghinii (Verany), Joubin, 1924: 68 (in part: only specimen from Sta. 3217).

Stigmatoteuthis arcturi Robson, 1948: 122, text-figs. 5, 6.

Calliteuthis dofleini, Dell, 1959: 100.—Clarke, M. R., 1962b: 439, pl. 15, fig. D.—Taki, 1964: 290.—Clarke, M. R., 1966: 198.

Calliteuthis sp., G. Voss, 1960: 427.

Histioteuthis dofleini, G. Voss, 1967: 74.

Material Examined.—HOLOTYPE OF *Stigmatoteuthis Chuni* PFEFFER: 1 ♀, ML 15.5 mm, VALDIVIA Sta. 235, 4°34'S, 53°42'E, 0-2000 meters.

HOLOTYPE OF *Stigmatoteuthis arcturi* ROBSON: 1 ♀, ML approx. 32 mm, ARCTURUS Sta. 7, 26°54'N, 51°15'W, 0-2990 meters, BM 1947.7.7.1.

OTHER MATERIAL: 1 ♀, ML 95.4 mm, OREGON Sta. 3726, 28°56.5'N, 88°46'W, 24 Aug. 1962, 403 meters.—1 ♂, ML 72.3 mm, OREGON Sta. 3733, 28°58'N, 88°37'W, 25 Aug. 1962, 403 meters.—2 sex ?, ML 70 + to 63 mm, off Miami, from stomach of *Alepisaurus* sp.—1 ♀, 68.0 mm, ELTANIN Sta. 1803, 39°36'S, 125°19'W, 24 Aug. 1966, ca. 600 meters, 3-m IKMT.—1 ♀, ML 63.0 mm, OREGON Sta. 3175, 29°03'N, 88°30'W, 11 Jan. 1961, 132 meters, UMMML 31.385.—1 ♀, ML 60.3 mm, U. of Wash. Sta. BB254 (between 5 and 6), 21 March 1960, mw 1400, coll.

Aron.—2 ♀♀, 7 ♂♂, ML 53.4-22.1 mm, OREGON Sta. 3258, 29°04'N, 87°39'W, 28 Apr. 1961, 183 meters, UMML 31.392.—2 ♀♀, 4 ♂♂, ML 49.7-38.2 mm, SIO C6303-Cobb58-21, 31°00'N, 119°32'W, 19 Mar. 1963, 457 meters, coll. F. Berry.—1 ♂, ML 48.0 mm, ALBATROSS Sta. 3476, 21°09'N, 157°53'W, 6 Dec. 1891, 550 meters, USNM 575000.—2 ♂♂, ML 48.0-39.3 mm, SILVER BAY Sta. 3459, 29°03'N, 78°05'W, 2 Oct. 1960, 914 meters, UMML 31.419.—1 ♂, ML 46.0 mm, SILVER BAY Sta. 4369, 29°07'N, 80°01'W, 29 Sept. 1962, 348 meters, UMML 31.452.—4 ♀♀, 1 sex ?, ML 43.0-19.5 mm, DANA Sta. 4176 I, 35°29'N, 21°00'W, 6 June 1931, mw 1000.—4 ♀♀, 2 ♂♂, ML 45.5-20.7 mm, OREGON Sta. 3296, 28°36'N, 89°48'W, 21 Aug. 1961, 446-954 meters, UMML 31.391.—1 ♀, ML 42.0 mm, ATLANTIS Sta. RHB 584, 18°55'N, 66°10'W, 4 March 1954, UMML 31.192.—1 ♀, ML 41.7 mm, SIO C6303-Cobb58-7, 32°07'N, 122°39'W, 6 March 1963, 640 meters.—1 ♀, ML 40.3, OREGON Sta. 3218, 29°11'N, 87°47'W, 9 Feb. 1961, 832 meters, UMML 31.418.—4 ♀♀, 13 ♂♂, 4 sex ?, ML 40.0-10.7 mm, OREGON Sta. 2944, 27°40'N, 90°50'W, 24 Aug. 1960, 183-229 meters, UMML 31.386.—7 ♀♀, 4 ♂♂, 6 sex ?, ML 38.0-14.0 mm, OREGON Sta. 2945, 28°33'N, 88°48'W, 25 Aug. 1960, 183-229 meters, UMML 31.387.—2 ♀♀, 1 ♂, ML 36.3-25.8 mm, OREGON Sta. 3219, 29°06'N, 88°02'W, 2 Sept. 1961, 274 meters, UMML 31.388.—1 ♀, ML 36.0 mm, DANA Sta. 4180 V, 32°56'N, 23°47'W, 8 June 1931, mw 2500.—1 sex ?, ML 34.8 mm, OREGON Sta. 1426, 29°07'N, 87°54'W, 29 Sept. 1955, 1100 meters.—1 ♀, ML 34.5 mm, ATLANTIS Sta. RHB 591, 25°32'N, 77°15'W, 22 Mar. 1954, 524 meters, UMML 31.191.—1 ♂, ML 33.0 mm, OREGON Sta. 2824, 29°7.5'N, 88°04'W, 17 July 1960, 667-723 meters, UMML 31.389.—4 ♀♀, 2 ♂♂, 8 sex ?, ML 32.8-16.5 mm, OREGON Sta. 3254, 29°00'N, 88°02'W, 27 April 1961, 247 meters, UMML 31.384.—2 spec., ML 28.0-20.3 mm, SILVER BAY 5071, 29°59'N, 88°35.5'W, 27 June 1963, 22 meters.—1 ♂, ML 26.0 mm, ATLANTIS Sta. 154, 21°05'N, 66°06'W, 6 Mar. 1949, UMML 31.421.—1 ♀, ML 26.0 mm, DANA Sta. 1365 XII, 31°47'N, 41°41'W, 8 June 1922, mw 3000.—2 ♀♀, 4 ♂♂, ML 25.2-20.0 mm, DANA Sta. 4180 VI, 32°56'N, 23°47'W, 8 June 1931, mw 1000.—1 ♀, 2 ♂♂, 4 fragments, ML 23.5-22.0 mm, OREGON Sta. 3362, 29°10'N, 88°21'W, 26 Sept. 1961, 267-874 meters.—1 ♀, ML 22.5 mm, ATLANTIS Sta. RHB 555, 25°26'N, 16°03'W, 10 Feb. 1954, 560 meters, UMML 31.193.—1 sex ?, ML 21.3 mm, SILVER BAY Sta. 445, 28°03'N, 78°44'W, 6 Sept. 1958, 915-950 meters.—1 ♀, ML 19.7 mm, DANA Sta. 1142 X, 33°26'N, 16°59'W, 15 Oct. 1921, mw 1000.—1 ♂, 1 sex ?, ML 18.9-15.4 mm, DANA Sta. 1361 I, 27°07'N, 51°10'W, 4 June 1922, mw 1000.—1 ♂, ML 18.3 mm, DANA Sta. 1334 I, 27°28'N, 59°29'W, 7 May 1922, mw 1000.—1 sex ?, ML 18.3 mm, DANA Sta. 1339 I, 30°00'N, 64°38'W, 10 May 1922, mw 1000.—1 ♂, ML 18.0

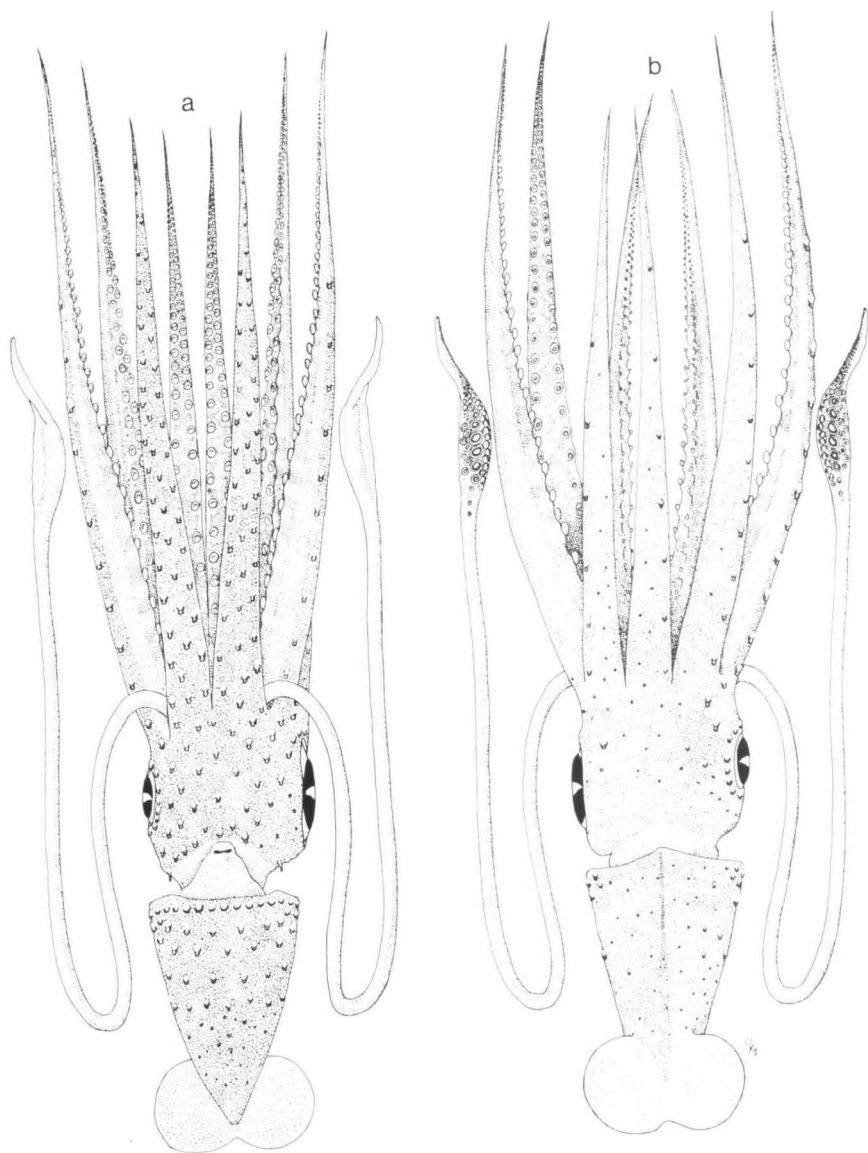


FIGURE 21. *Histoteuthis dofleini* (Pfeffer, 1912), Elt 1803, ML 68.0 mm:
a, ventral view; b, dorsal view.

mm, DANA Sta. 1326 I, 27°14'N, 51°25'W, 2 May 1922, mw 1000.—1 ♀, ML 17.5 mm, OREGON Sta. 3437, 29°11'N, 87°55'W, 21 Nov. 1961, 695-1098 meters.—2 ♀♀, ML 16.6-13.0 mm, DANA Sta. 1358 VIII, 28°15'N, 56°00'W, 3 June 1922, mw 1000.—1 ♀, ML 16 mm, PRINCESSE-ALICE Sta. 3217, 30°45'30"N, 25°47'W, 8 Aug. 1912, 0-1000 meters.—1 sex ?, ML 16.0 mm, U. of Wash. Sta. BB-199-157 (between 15-16) off Washington coast, 19 July 1958, 120 meters, Coll. Aron.—1 ♀, ML 15.1 mm, DANA Sta. 1328 VIII, 27°05'N, 52°11'W, 3 May 1922, mw 900.—1 ♀, ML 15.0 mm, DANA Sta. 1242 VIII, 24°05'N, 74°36'W, 15 Feb. 1922, mw 1000.—1 ♀, ML 15.0 mm, IKMT No. 34, 25°30'S, 40°40'E, 18 Aug. 1962, 500 meters, SAM A29698.—1 ♀, ML 15.0 mm, DANA Sta. 1332 XIII, 26°58'N, 56°58'W, 6 May 1922, mw 1000.—1 ♀, ML 13.6 mm, DANA Sta. 1335 I, 28°02'N, 62°26'W, 8 May 1922, mw 1000.—1 ♀, ML 13.3 mm, IKMT No. 46, 26°42'S, 40°07'E, 22 Feb. 1963, 500 meters, SAM A29750.—1 sex ?, ML 13.2 mm, DANA Sta. 1358 IV, 28°15'N, 56°00'W, 2 June 1922, mw 4000.—1 sex ?, ML 11.8 mm, DANA Sta. 1190 VI, 17°58.5'N, 64°45'W, 13 Dec. 1921, mw 1000.—1 sex ?, ML 11.4 mm, DANA Sta. 1320 II, 23°18'N, 56°58'W, 27 Apr. 1922, mw 800.—3 sex ?, ML 10.9-6.7 mm, DANA Sta. 4017 VIII, 29°13'N, 14°12'W, 27 Mar. 1930, mw 600.—2 sex ?, ML 10.6-7.0 mm, DANA Sta. 1328 I, 27°05'N, 52°11'W, 3 May 1922, mw 700.—1 sex ?, ML 10.5 mm, DANA Sta. 1362 II, 28°57'N, 47°24'W, 6 June 1922, mw 600.—1 sex ?, ML 9.5 mm, DANA Sta. 1161 IV, 14°52'N, 28°04'W, 5 Nov. 1921, mw 300.—1 sex ?, ML 9.0 mm, DANA Sta. 1185 VIII, 17°41'N, 60°58'W, 27 Nov. 1921, mw 1000.—2 sex ?, ML 9.0-8.5 mm, DANA Sta. 1328 IX, 27°05'N, 52°11'W, 3 May 1922, mw 800.—1 sex ?, ML 8.8 mm, DANA Sta. 4009 II, 24°36'5"N, 17°27'W, 18 Mar. 1930, mw 600.—1 sex ?, ML 7.8 mm, DANA Sta. 4023 V, 35°06'N, 7°01'W, 8 Apr. 1930, mw 500.—1 sex ?, ML approx. 7 mm, DANA Sta. 1334 II, 27°28'N, 59°29'W, 7 May 1922, mw 600.—1 sex ?, ML 6.9 mm, DANA Sta. 1330 III, 26°37'N, 54°45'W, 4 May 1922, mw 600.—1 sex ?, ML 6.5 mm, DANA Sta. 4180 VII, 32°56'N, 23°47'W, 8 June 1931, mw 600.—2 sex ?, ML 6.2-4.5 mm, MMF 18121 A-B, Câmara de Lobos, Madeira Islands, 15 Dec. 1960, from stomach of *Alepisaurus ferox*.—1 sex ?, ALBATROSS Sta. 4687, E. Pac. Exped. 1904-05, 22°49.5'S, 97°30.6'W, surface, USNM.

Description.—*Skin* of whole body often thickly beset with low fleshy papillae, giving overall rough appearance.

Mantle conical, with moderately heavy walls, and blunt posterior tip; width slightly greater than half mantle length; greatest width just posterior to anterior margin. Anteroventral margin slightly excavated beneath funnel with blunt lateral angles; anterodorsal margin produced medially to strong

blunt obtuse angle; left anterolateral margin more emarginate than right.

Fins transversely oval, united posteriorly with shallow median notch; posterior margin extending short distance beyond free tip of mantle. Moderately large, fin length about 35-46 per cent of mantle length; width about 63-70 per cent of mantle length.

Funnel strong with thick ventral wall, bifurcate dorsal support. Mantle member of *funnel-mantle locking apparatus* crescent-shaped ridge, narrow anteriorly, broad posteriorly; slightly curved groove in funnel cartilage deep, narrower anteriorly than posteriorly. Dorsal member of *funnel organ* inverted V-shaped pad with long narrow arms; strong ridge running medially down each from anterior apical papilla expanding into broad flap on posterior half of arm; two large oval ventral pads present. *Valve* large, semicircular.

Head large, wider than mantle, asymmetrical, with left eye two to three times size of right. *Sinus* in anterior margin of both eyelids. No *nuchal folds* apparent. *Olfactory organ*, papilla extending up from fleshy lobe.

Buccal membrane seven-membered with support attachments as follows: middorsal or first support bifurcate to dorsal sides of arms I; second supports to dorsal sides of II; third supports to ventral sides of III; fourth supports to dorsal sides of IV.

Outer web may or may not be developed up to depth of about 14 per cent length of longest arm. *Inner web* very low to vestigial.

Arms long, up to about two and a half times mantle length; stout basally, tapering gradually to slender tips. Second and third arms about coequal; first and fourth arms slightly shorter, about coequal; resultant arm formula $2 = 3.1 = 4$. Low, median *swimming keel* originating at about midarm on aboral surface of III; after about one-quarter length of arm diminishing to low median ridge to tip of arm. Arms I, II, and III appear to bear low median keels terminally.

Suckers on arms biserial, seated on distinct platforms, outer edges of which continuous with strong marginal *protective membrane*, giving crenulated effect to margin of membrane. At about midarm, membrane with complete breaks between suckers. Suckers of I, II, and III largest in second third of arm length, thereafter gradually diminishing to minute size on tip. Suckers of IV about coequal in size, about one-third size of those of other arms.

Horny rings of suckers I, II, and III usually with 14-28 small round or square teeth on distal or entire margin. Teeth on distal suckers usually more distinct. Rings of IV usually more toothed than other arms.

Both arms I of large males *hectocotylized*. In affected portion, terminal quarter to third of arm heavier than normal, with two rows of suckers at first widely spaced; enlarged pedestals closely set marginally giving palisade effect in side view.

Tentacles strong, long, up to four times mantle in length. *Club* with expanded manus, long narrow dactylus. On aboral surface of club, anterior half may or may not have longitudinal *cleft*; posterior half with median *swimming keel*. Aborally, tentacular stalk usually with strong median ridge for short distance prior to club.

Suckers of manus in rows of 5-7, with strong dissimilarity in size. Suckers of two median rows largest, up to three times size of remaining suckers; suckers of marginal row on either side minute. Suckers on slender dactylus uniformly small; rows reduce to three near terminal pad. *Protective membrane* marginal on either side of manus, diminishing abruptly on dactylus.

Horny rings of larger suckers of manus usually with about 50-70 strong pointed teeth on entire margin. Moderately large suckers of second row from ventral margin with horny accessory growth from dorsal side of base of ring. Dentition of these latter suckers irregular, ranging from small to large heavy teeth.

Carpal adhesive apparatus extending on oral surface of tentacular stalk to about one and one-half club-lengths proximal to club. From this point proceeding toward club, arrangement as follows: single small sucker (1 s), followed by two widely spaced pads (2 pp), then 2 ss, 2 pp, 2 ss in single row along ventral margin of stalk; crossing over and straddling median line, arrangement continues with pairs of elements of unequal size set diagonally in two rows, 2 pp, 2 ss, 2 pp, 2 ss; again in single row, up dorsal side of stalk, 1 p, 1 s, 1 p, 1 s (specimens from Pacific often with additional 1 p, 1 s) and enlarged pad (1 p) at base of manus; then 1 s, 1 p, 1 s, 1 p continue for short distance up dorsal margin of manus. Above arrangement on either tentacle, with mirror image on other, most typical of *dofleini* from Atlantic waters.

Photophores on ventral surface of mantle widely spaced, roughly set in about six diagonal rows, with exception of anterior marginal row; approximately nine photophores in diagonal row connecting at lateral angle. About equally large in size on anterior third of mantle with no intermixing of small photophores; thereafter regularly decreasing in size to minute photophores near posterior tip of mantle. Photophores on dorsal surface of mantle smaller, fewer in number, more widely spaced in diagonal rows.

Numerous large photophores on ventral surface of head set in diagonal rows except for circlet around eyelids. Seventeen large photophores forming closed circlet around margin of right eyelid; dorsalmost organ somewhat separated from others, two ventralmost organs somewhat more ventrally set; three or four small additional organs around ventral side of lid, one or two small additional organs on anterodorsal margin of lid. Photophores on dorsal surface of head, few large, mostly small, widely set in diagonal rows.

Arm IV with three rows of large photophores (two additional photo-

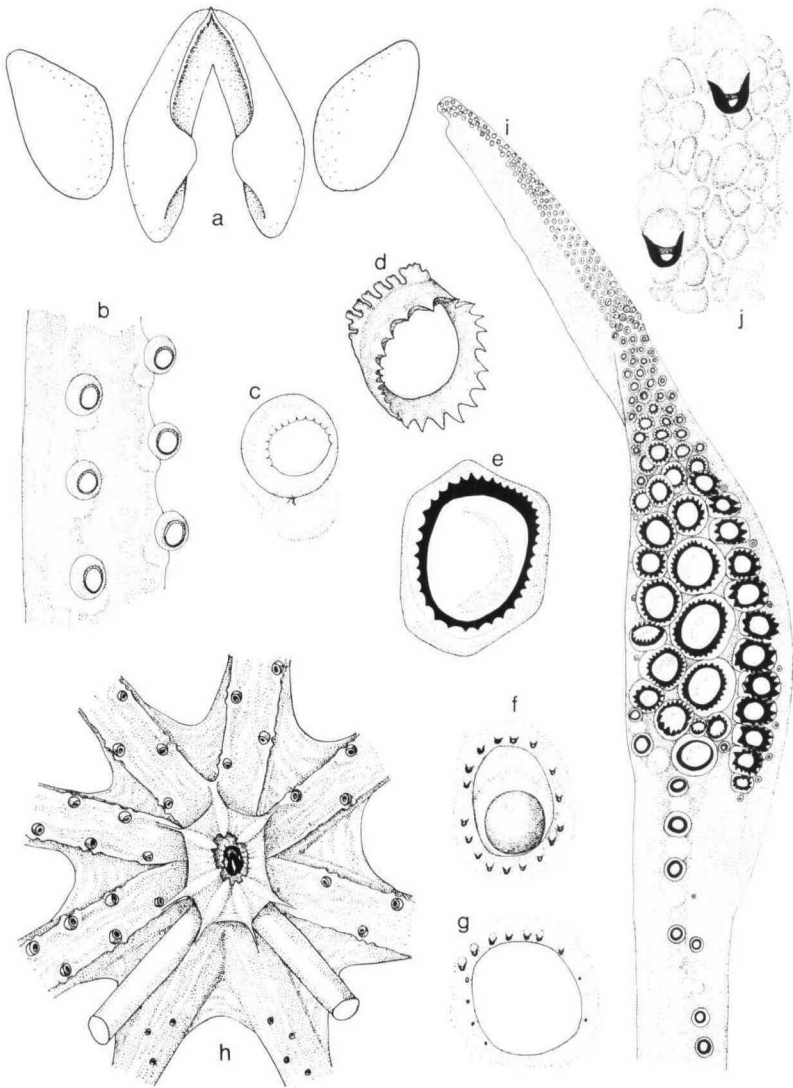


FIGURE 22. *Histioteuthis dofleini* (Pfeffer, 1912): a, funnel organ; b, section of arm III, *Elt* 1803, ML 68.0 mm; c, sucker from 6th row, arm III of same; d, club sucker ring, second ventral row, U. of Wash. Sta. BB254, ML 60.3 mm; e, largest club sucker, *Elt* 1803; f, right eyelid of same; g, left eyelid of same; h, buccal view, U. of Wash. Sta. BB254; i, left tentacular club, *Elt* 1803; j, section of skin from base of arm IV of same, showing typical irregular papillations.

phores on base of arm are not considered as comprising a fourth row), no dorsal margin row of small organs; median row extending to distal tip of arm; ventral row terminating short of tip; dorsal row of eight to eleven organs extending about two-thirds length of arm. Arms I, II, and III with two or three rows of photophores; ventral row of large organs extending to tip of arm; dorsal rows of very small organs shorter.

Male with double set of functional *genitalia*. Mature *spermatophores* found only in male of 72.3 mm ML (OREGON Sta. 3733). Spermatophore long, 10.56-11.12 mm, SpLI 0.146-0.154; SpWI 2.17-3.06. Ejaculatory apparatus long, EjAI 37.5-43.0; greatly coiled and twisted for most of its length except for short straight portion at oral end. Relatively short cement body, CBI 15.4-21.4, tapering orally into ejaculatory tube without apparent specific connective complex. Sperm mass long and slender, SpMI 38.7-42.6.

Gladius (GL 55.0 mm) delicate, lightly pigmented, ventral surface deeply concave. Vane long (GVLI 76.4), moderately broad (GVWI 24.8); posterolateral margins slightly thickened, more heavily pigmented. Rhachis ending in coil at posterior tip of gladius.

Upper *beaks* with obtuse false jaw angle. Lower beak with well-developed median ridge bisecting lateral wall.

Radulas of two specimens, one from South Pacific and one from Gulf of Mexico, illustrated. First and second laterals asymmetrical with rather short, broad bases. Marginal plates absent, except on one side of radula of specimen from South Pacific.

Type.—Whereabouts unknown.

Type-Locality.—Sagami Bay, Japan; surface.

Discussion.—In 1912, Pfeffer gave the name *Stigmatoteuthis Dofleini* to a large mature male specimen from Sagami Bay, Japan, first described by Chun in 1906 as *Calliteuthis reversa* Verrill; later (1910) Chun considered it to be identical with *Calliteuthis ocellata* (Owen). Though the type was never located, the description and illustrations given by Chun are more than sufficient to establish the name. In the same work (1912) and two pages earlier, Pfeffer gave the name *Stigmatoteuthis Chuni* to another specimen that Chun had described as *Calliteuthis Hoylei* in 1910. This was a small immature female that was inadequately described. However, the type was examined in Berlin by G. Voss and it appears to be the same as *Dofleini*. Though *Chuni* has page priority and the type is available, the completely inadequate first description and present condition of the specimen, too poor for redescription, together with its small size and immature state were considered sufficient reasons by the author for retaining *Dofleini* as the valid name.

I have delayed in naming a neotype for this species since it is possible

TABLE 8
MANTLE MEASUREMENTS (IN MM) AND INDICES OF *Histioteuthis doffeini* (PFEFFER, 1912)

	♂ O 3726	♂ BB254	♂ O 3258	♂ SIO-C6303 Cobb58-21	♀ O 3258	♂ SIO-C6303 Cobb58-21	♀ SIO-C6303 Cobb58-21	♂ SIO-C6303 Cobb58-21	♀ O 3296	♂ O 3296	♀ O 3296	♂ O 3296	♀ SIO-C6303 Cobb58-21	♂ SIO-C6303 Cobb58-21
ML	95.4	60.3	53.4	48.7	47.1	45.4	45.3	45.0	43.0	42.0	39.6	39.0	38.5	38.0
MLI	22.8	25.2	—	24.2	26.0	26.2	27.6	25.0	25.5	25.3	27.1	—	24.6	26.9
MWI	58.7	42.6	54.4	57.5	62.8	55.0	48.7	53.5	58.6	59.5	53.0	57.0	58.2	50.5
HLI	61.9	—	65.0	56.0	61.2	46.3	46.3	51.1	62.7	—	—	65.4	57.1	60.0
HWI	—	56.0	—	56.5	—	61.7	—	66.7	—	—	—	—	70.0	—
FLI	42.6	39.8	39.1	38.6	44.5	38.0	37.5	41.4	39.5	40.0	35.3	38.4	41.5	40.0
FWI	68.5	60.5	64.3	60.8	—	61.7	57.4	58.2	69.8	68.5	—	63.3	67.5	65.0
AI I	—	190.8	227.3	212.0	215.0	198.5	182.5	204.0	209.0	202.0	197.0	190.0	200.5	185.0
II	—	232.0	260.0	254.0	216.6	226.5	210.0	226.0	229.0	228.3	212.0	216.0	236.0	205.4
III	278.0	229.0	249.0	246.4	215.9	220.0	212.5	238.0	230.0	240.5	198.0	208.0	232.0	211.0
IV	232.0	189.0	206.0	207.3	198.4	183.0	171.6	199.5	191.0	196.5	179.2	178.0	212.0	187.0
TLI	—	195.0	—	357.0	332.0	302.0	280.0	345.3	326.0	—	326.0	—	278.0	308.0
CLI	—	39.8	—	43.2	47.5	41.2	39.3	43.7	40.8	—	42.9	38.2	43.7	35.8
M+I	10.9	6.6	9.5	12.3	10.6	7.1	7.3	10.7	9.5	—	—	6.9	7.8	12.9
OWI A	2.6	9.8	—	10.1	3.7	9.8	9.2	9.6	—	—	—	—	10.3	12.0
B	3.4	11.4	4.2	13.1	4.1	11.9	11.2	7.7	5.1	5.9	6.2	—	11.3	11.4
C	3.4	13.5	6.7	13.1	5.5	12.0	11.7	6.8	7.4	8.3	9.1	7.2	7.8	11.8
D	5.5	12.9	—	8.7	—	9.8	6.2	5.4	8.1	6.6	9.6	7.2	9.9	—
E	2.3	9.7	—	6.7	—	7.3	7.5	—	—	—	—	—	5.3	—

TABLE 8 (Continued)

MANTLE MEASUREMENTS (IN MM) AND INDICES OF *Histioteuthis dosseini* (PFEFFER, 1912)

[illegible]

that the holotype lies forgotten on a shelf in Leipzig, the scene of Chun's work.

In examining Joubin's material at Monaco in the summer of 1961, one of his specimens listed in his 1924 report under *Calliteuthis Meneghinii* (Verany) was found to be *H. dofleini*. In his description, Joubin had singled out this specimen, noting the smaller number of photophores on the mantle and the regular reduction in their size as they approach the posterior tip. This is one of the easily observable distinguishing characters of this species when compared with *H. reversa*; the remainder of his material listed under *C. Meneghinii* belonged to *H. reversa* as determined by the present author.

In 1948, Robson named a new species, *Stigmatoteuthis arcturi*, based on a specimen collected in mid-North Atlantic by the ARCTURUS. The type was examined in London and without a doubt is synonymous with *H. dofleini*.

A juvenile specimen from Bermuda referred to by G. Voss (1960) as *Calliteuthis* sp. was found to be *H. dofleini*. Undoubtedly many other specimens unavailable to the writer, which are listed but undescribed, or inadequately described in the literature under another species or as "sp.," will prove to belong to *H. dofleini*, which apparently is one of the commonest and mostly widely distributed members of the genus.

Histioteuthis dofleini (Pfeffer) displays several characters so far unique within the genus. One is the double set of functional genitalia in the male, and another is the distinct flap formation on the dorsal pad of the funnel organ. The "rough" or papillated skin seems to be a unique character (though it is not apparent on all specimens) along with the accessory horny projections, discussed later, on the rings of certain of the tentacular suckers. The additional confirming combination of characters for *H. dofleini* is the relatively short, broad, conical mantle; the very long arms (to two and a half times the mantle length); the pattern of widely set photophores on the anterior third of the mantle, with no intermixing of small organs, and the regular decrease in size of the organs to near the mantle tip; 17 large photophores around the right eyelid (one otherwise normal individual had 16); the arrangement of light organs around the left eyelid described above; and the three rows of photophores on arms IV.

Several characters in *H. dofleini* display quite a degree of variation. Though the inner web is very low to vestigial, an outer web is often developed. In a number of individuals 38.0-60.3 mm ML in size, from off the West Coast of the United States, the outer web was conspicuously developed to a depth of 9.6 to 13.5 per cent of the length of the longest arm; in Atlantic specimens of the same size range, the maximum depth of this outer web was 5.5 to 9.6 per cent of the length of the longest arm. The dentition of the arm suckers varies considerably. In the majority, the

teeth were confined to the distal margin of the rings, but a few specimens had the entire margin incised. The average number of teeth ranged between 14 and 28 but some individuals had as few as six teeth. No individual examined had completely smooth rings.

The teeth on the rings of the larger tentacular suckers were seldom uniform around the entire margin; usually, they were small and closely set on the dorsal margin and large, heavy, and widely set on the ventral margin, often tending to flare out. The moderately large suckers of the second row from the ventral margin, referred to by Sasaki (1916: 101) as "ventral submedian," appear to have increasingly irregular dentition with increase in size of the individual, and some of the teeth become disproportionately large. These same suckers have a unique accessory growth from the dorsal side of the base of their horny rings. This accessory growth, in the form of a rectangular (or in some a triangular) shelf, is made up of several teeth, often branched, or knobs set in a single plane. In a number of the Pacific specimens from off the Washington and California coast and in the ELTANIN specimen from the South Pacific, the six or seven teeth are well developed in a regular series, but in the Atlantic specimens the teeth tend to be fewer and less regular in shape and often are mere knobs. In the 48.0-mm-ML specimen from the Hawaiian Islands, the growth is three membered and nearly triangular, composed of a large, heavy, irregularly shaped central projection with single lateral knobs. These accessory horny growths are usually obscured by the opaqueness of the overlying flesh and thus are easily overlooked. The growth is not developed in the juveniles.

H. dofleini has the largest spermatophores yet found in the family. The multiple coiling of the ejaculatory tube found in all of the spermatophores of the male from the Gulf of Mexico (only male available with spermatophores) is unusual. Marchand (1913), Chun (1910) (same as illustrated and described by Marchand), and Sasaki (1929) illustrated the spermatophore of *dofleini* from Japanese waters. It compares well with that of the specimen from the Gulf of Mexico in size, relative proportion of the parts, and in the fact that there is no specific connective complex between the cement body and the ejaculatory apparatus, but it varies in that the ejaculatory tube is twisted into a single large loop instead of the multiple coiling found in the male from the Gulf of Mexico. The significance of this variation must await the study of additional material from the same and intervening geographic areas. At this point of our knowledge, I do not consider it sufficient for taxonomic distinction.

The most obvious proportional change accompanying growth in this species is the disproportionate lengthening of the arms. The flaplike projection on the dorsal pad of the funnel organ is usually apparent in juveniles as small as about 7 mm mantle length; below this size, the pad

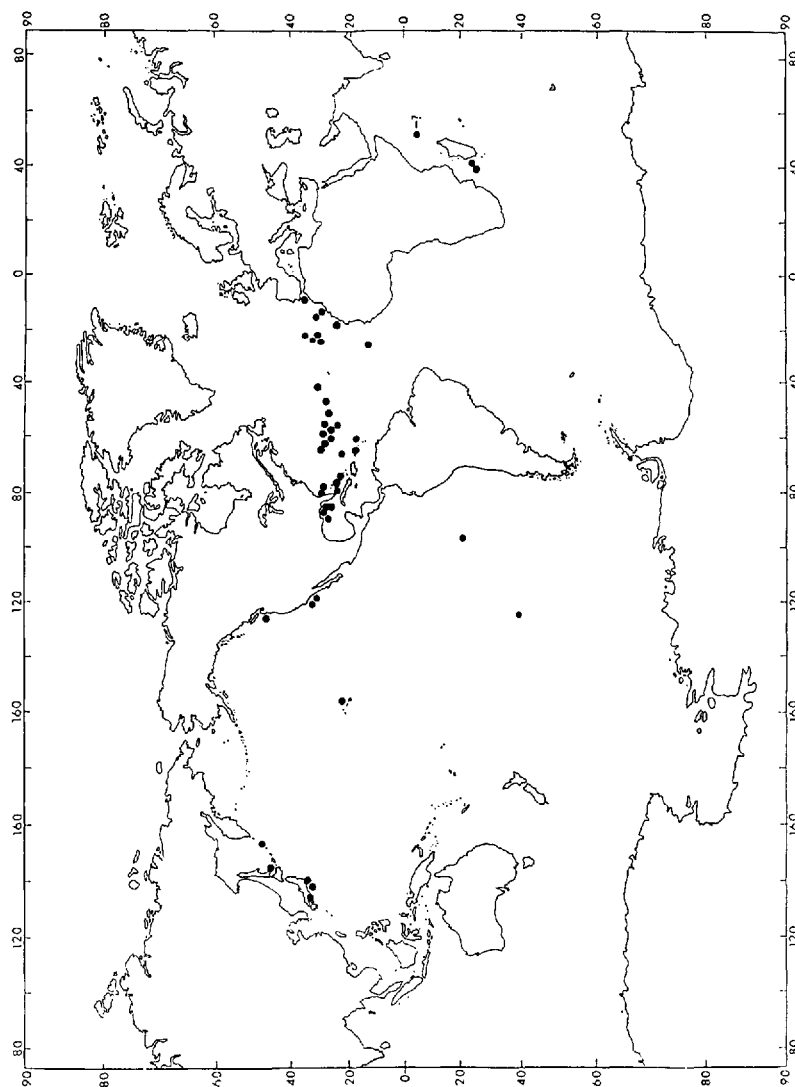


FIGURE 23. Distribution of confirmed, identified specimens of *Histioteuthis dofleini* (Pfeffer).

usually has only a median ridge extending down each arm from the apical papilla.

Chun (1906, 1910) described and illustrated the hectocotyization of both dorsal arms of the male type, and Sasaki (1929) confirmed the condition in his males. All of their specimens were large, in excess of 100 mm ML. The males studied by the author were small in comparison, and only the largest specimens (73.2 to 38.5 mm ML) showed hectocotyization. This, as would be expected, was developed to a lesser degree. In addition, Chun (1906, 1910) illustrated the double genitalia of the type.

The numerous specimens herein referred to *dofleini* most probably represent two or more subspecies. Since, however, *dofleini* was found to be the most inconsistently variable of all the histioteuthids, the available material was considered inadequate to resolve the problem clearly at this time.

Remarks.—Sasaki (1916, 1929) gave the Japanese name for *dofleini*, “kuragedako,” meaning jellyfish octopus (Taki, 1964).

Distribution.—The specimens herein referred to *H. dofleini* (Pfeffer) have been collected from throughout the North Atlantic between the latitudes of 15° and 36°N, and in the Gulf of Mexico; from the North Pacific off the United States and Baja California, in the vicinity of the Hawaiian Islands, off the east coast of Japan and in the Sea of Japan; and from the eastern South Pacific. In the Indian Ocean, *dofleini* has been taken in the vicinity of the Seychelles and between Natal and Madagascar.

The numerous catches in the Sargasso Sea comprise the only record of a histioteuthid that has been taken in any abundance in midoceanic waters unrelated to oceanic ridges. This same squid also occurs in large numbers in the Gulf of Mexico at the mouth of the Mississippi River.

Throughout its distribution, *dofleini* appears to be most concentrated in the upper 700 or 800 meters of water.

Histioteuthis miranda (Berry, 1918)

Figs. 24, 25, 27

Calliteuthis miranda Berry, 1918: 221, pls. 61, 62, text-figs. 5-9.—Cotton & Godfrey, 1940: 388, figs. 381-383.—Clarke, M. R., 1966: 199.

?*Histiothauma oceani* Robson, 1948: 123, text-fig. 7.—Dell, 1959: 98.

Material Examined.—NEOTYPE: 1 ♀, ML 182.0 mm, ELTANIN Sta. 1713, 37°54'S, 178°56'E, 28 May 1966, 448-732 meters, 40-foot otter trawl, USNM 576165.

OTHER MATERIAL: 1 ♀, ML 17.0 mm, TUI Oceanographic Cruise, 32°27'S, 174°11.5'E, 5 July 1962, 49 meters (in scattering layer), AUZ 080.04.—1 ♀, ML 17.0 mm, SIO Troll 30, 5°58'N, 127°23'E, 1 April 1955, 140 meters.—1 spec., ML 7.2 mm, ARCTURUS Sta. 51-T2, 2°33'S,

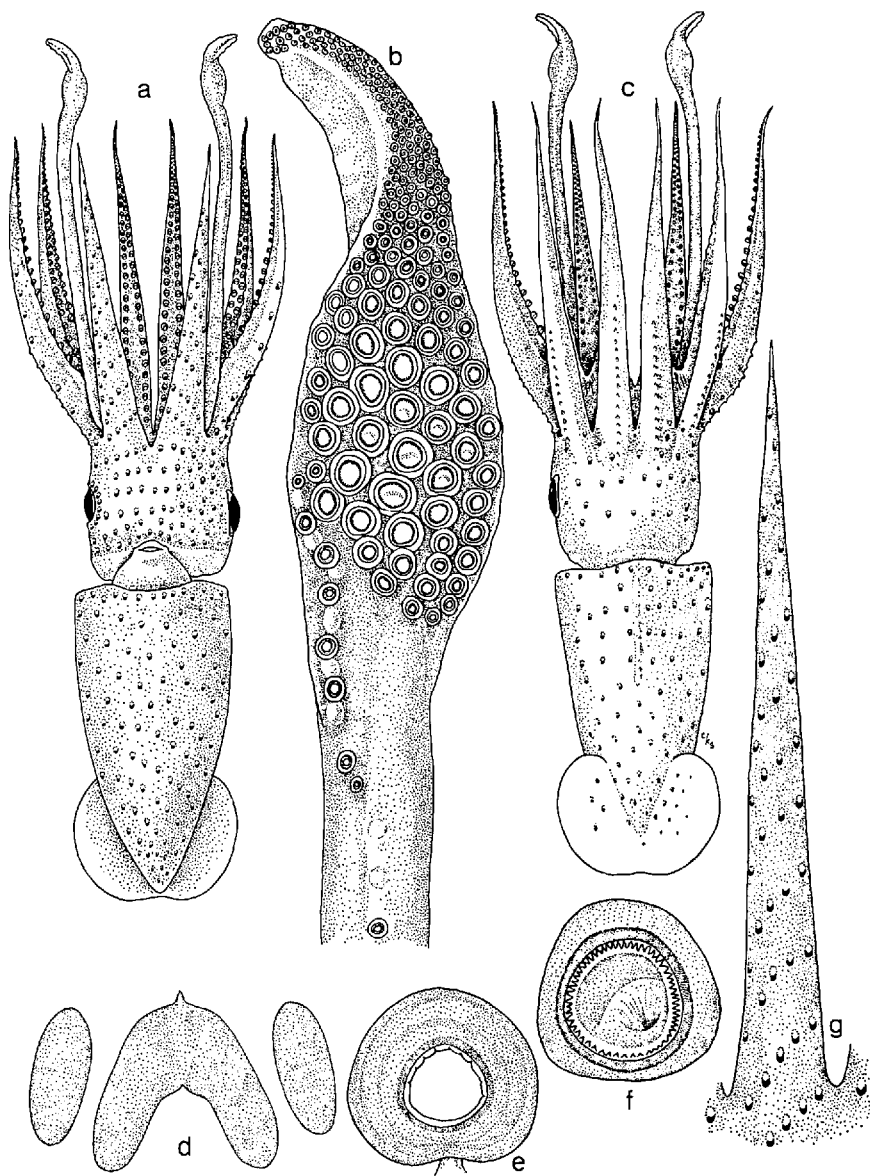


FIGURE 24. *Histioteuthis miranda* (Berry, 1918), neotype, USNM 576165, ML 182.0 mm: a, ventral view; b, left tentacular club; c, dorsal view; d, funnel organ; e, sucker, midarm III; f, largest tentacular sucker; g, right arm IV.

89°44'W, 23 April 1925, 0-300 meters, BM 1947.7.8.95 (Holotype of *Histioteutha oceani* Robson).

Description.—*Mantle* conical, robust, walls thick, width approximately half mantle length; widest point just posterior to anterior margin, thence sides taper to blunt posterior tip. Median anterodorsal margin produced into low obtuse angle; median anteroventral margin only slightly emarginate between blunt lateral angles. Ridge of low *tubercles* beneath epithelium extending along median line of dorsum from just below anterior margin of mantle to approximately one-half the distance to posterior tip.

Fins combined, semicircular in outline; length slightly less than half mantle length, width slightly more. Posterior margins of lobes exceed tip of mantle, join with median notch.

Funnel stout with double bridle. *Locking apparatus* strong, typically histioteuthid; central groove in funnel member very deep. Dorsal member of *funnel organ* fleshy but unsculptured with anterior apical papilla; two ventral pads large, oval. *Valve* large, semicircular.

Head large, with typical asymmetrical eyes, the left eye being approximately twice the size of the right; apparently a single *nuchal fold* dorsal to small *olfactory papilla*.

Buccal membrane seven-membered. Middorsal or first support bifurcate through web to dorsal side of arms I; second supports bifurcate through web to ventral side of I and dorsal side of II; third supports to ventral side of III; fourth supports to dorsal side of IV.

First three pairs of arms joined basally for approximately one-quarter of length by *inner web*; *outer web* slightly developed.

Arms one to one and a half times mantle in length, stout basally, thence tapering to slender tips. Arms II and III longest, approximately coequal; arms IV shortest. Short expanded *swimming keel* at midlength on aboral surface of arms III. In neotype, aboral surfaces of I, II, and III each with median row of *tubercles* beneath epithelium for approximately one-third to one-half length of arm. *Keels* on distal portions of aboral surfaces of arms not apparent.

Two rows of widely set *suckers* on sessile arms. Suckers roughly coequal in size, except near tip of arm. Distal margins of horny rings with about eight to twelve low square teeth, often with obscure demarcation; proximal margins ragged to smooth.

Tentacles stout, moderately long, about a third longer than sessile arms. *Club* expanded; manus with about six or seven rows of closely set suckers; median few suckers of two dorsomedian rows slightly enlarged. Horny rings armed around entire margin with numerous small sharp teeth; largest suckers with about 45-50 teeth. Suckers on dactylus uniform, very small, crowded at first into six or seven rows, reducing to about four near terminus.

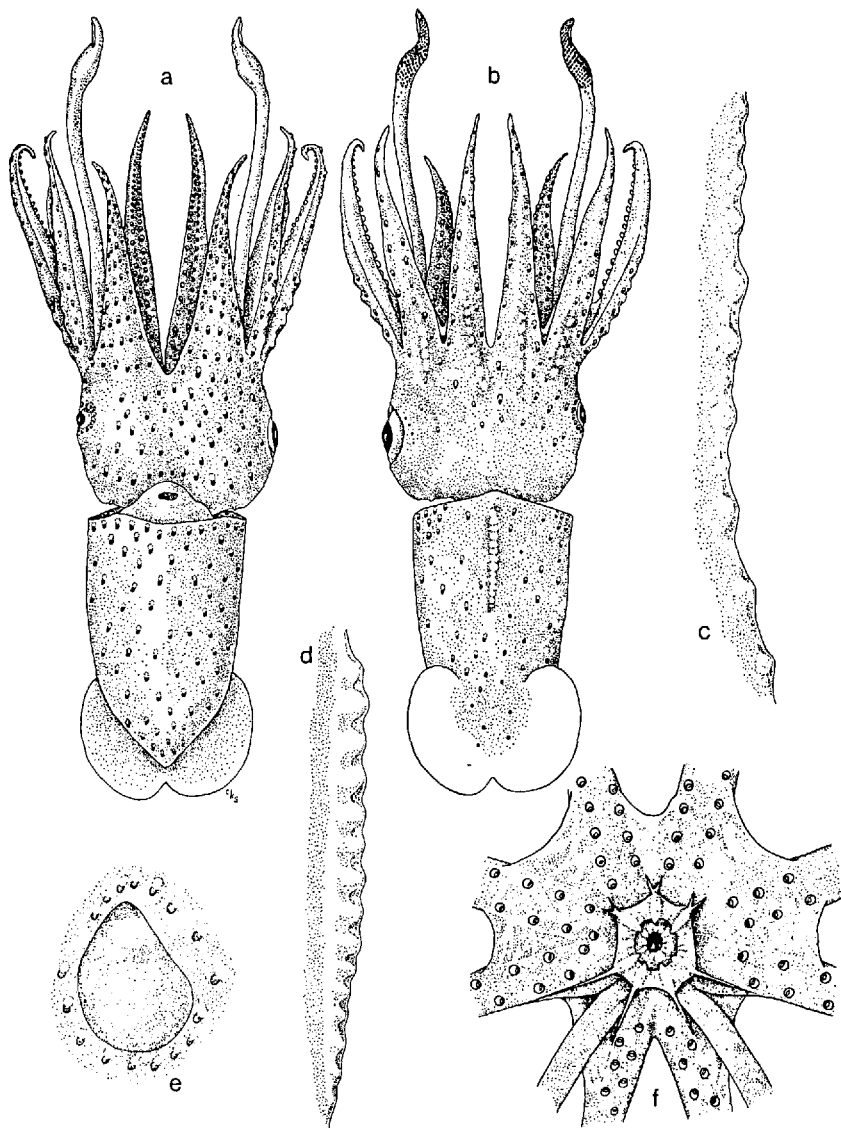


FIGURE 25. *Histioteuthis miranda* (Berry, 1918): a, ventral view, AUZ 080.04, ML 17.0 mm; b, dorsal view of same; c, lateral view of tubercles on left arm I of same; d, lateral view of tubercles on dorsal surface of mantle of same; e, margin of right eyelid, neotype; f, buccal view of same.

Terminal half of aboral surface of club with median *swimming keel*; no longitudinal *cleft* apparent on proximal half.

At point approximately one and three-quarters of a club-length proximal to base of club, *carpal adhesive apparatus* on the left tentacle of neotype as follows: small suckers (1 s), followed by 2 pp and 2 ss widely set, then more closely set 2 pp, 2 ss, 2 pp, then crossing diagonally to dorsal margin, 2 ss, 2 pp, and up dorsal margin of stalk onto dorsal margin of manus, 6 ss, alternating singly with 5 pp; entire arrangement uniserial.

Numerous *photophores* set in roughly nine or ten diagonal rows across entire ventral surface of mantle except for closely set anterior marginal row. Photophores moderately widely spaced, about twelve in diagonal row commencing at lateral angle, uniformly set down anterior three-quarters; no intermixture of sizes. Average photophore on 182-mm-ML neotype measured about 3.6 mm in length. Photophores on dorsal surface of mantle and head markedly fewer and smaller.

Photophores on ventral surface of head of same approximate size and concentration as on ventral surface of mantle; set in diagonal rows except for posterior marginal row and circumocular rows. Sixteen or 17 (17 in neotype) large photophores in complete circlet around right eyelid margin; pattern around left eyelid margin not distinct in available material. Base of arms IV with five longitudinal rows of photophores; as arm tapers, rows reduce gradually to two with only one, originally the second ventral row, extending to tip. Arms III, II, and I with two or three longitudinal rows of photophores.

No males available for description of *hectocotylus*, *genitalia*, or *spermatophores*. Uniqueness of material prevented examination of *gladius*, *beaks*, and *radula*. Berry (1918) described and illustrated the beaks and radula of his holotype. A sharp median ridge is present on lateral wall of lower beak.

Neotype.—United States National Museum, USNM 576165.

Neotype Locality.—South Pacific, 37°54'S, 178°56'E, 732-448 meters.

Discussion.—Berry (1918) described *Calliteuthis miranda*, now *Histioteuthis miranda*, from a unique specimen, a large female of 140 mm ML, collected by the ENDEAVOUR off Gabo Island, Victoria, Australia. The type was deposited in the Australian Museum, Sydney (No. E5606). In correspondence with Dr. Donald F. McMichael, Curator of Molluscs of the Australian Museum, I was informed that Berry's specimen had dried up in the past and is no longer extant. Thus the present large female, herein described and illustrated, is named as neotype for the species.

The neotype compares well with Berry's specimen, varying only in the number of photophores around the margin of the right eyelid (17 in the neotype, 16 in the holotype) and in the number of elements in the carpal

TABLE 9
MANTLE MEASUREMENTS (IN MM) AND INDICES OF
Histioteuthis miranda (BERRY, 1918)

	Neotype <i>Elt</i> 1713 ♀	Holotype* AM E5605 ♀	AUZ 080.04 ♀	SIO Troll 30 ♀
ML	182.0	140	17.0	17.0
MWI	53.3	50.0	60.0	60.0
HLI	34.7	—	48.8	47.0
HWI	48.4	—	70.5	71.1
FLI	38.5	42.8	48.8	40.6
FWI	54.5	53.6	74.0	60.0
AI I	—	139.3	91.0	140.0
II	107.2	143.0	103.0	153.0
III	103.3	143.0	100.0	147.0
IV	96.7	132.0	87.0	115.5
TLI	147.2	185.8	141.2	149.0
CLI	21.4	25.0	26.4	31.2
M+I	—	—	15.9	13.0
IWI A	22.1	25.0	16.9	9.6
B	29.2	—	18.3	11.5
C	29.7+	—	23.4	13.1

* No longer extant; indices from original measurements of Berry (1918: 226).

arrangement; the neotype has one or two more pads and suckers. Either variation is occasionally encountered in a group of any one species in the histioteuthids. The locality of capture of the neotype just east of New Zealand is not far geographically from that of Berry's holotype off Victoria, Australia.

Despite the very poor condition of his specimen, Berry recognized and described fully its unique distinguishing characters, which are the median tubercular rows on the dorsum of the mantle and on the first three pairs of arms, similar to those of *H. meleagroteuthis*, and the pattern of photophores, which varies from that of *meleagroteuthis* in the lesser concentration and larger relative size of photophores on the surface of the mantle, head, and arms. Though the poor condition did not permit an accurate description or illustration of the complete pattern, Berry could distinguish the important features of five longitudinal rows of photophores on the bases of the ventral arms. An additional character which Berry considered to be of importance in *miranda*—the base of the tentacle being anchored by a muscle cord originating from a special pouch adjacent to the buccal membrane—is not unique, however, but rather is found in all histioteuthids and possibly in all species of squids.

The added two specimens available to me, both small juveniles of 17

mm ML, one from just north of New Zealand and the other from the Philippine Sea, were in near perfect condition. The juvenile from the Philippine Sea was in a more distended state than the New Zealand one, hence the marked differences in the indices for the arm lengths and web depths. This same specimen also has the median row of tubercles on the arms more developed; the tubercles extend up for three-quarters of the length of all three pairs of dorsal arms, rather than for just one-third to one-half as in the juvenile from New Zealand. Berry described his large holotype of 140 mm as having tubercles on the basal quarters of the first arms and but traces on the bases of the second and third arms. Since his specimen was in such poor condition, the distal portions of the rows of tubercles were more than likely destroyed, for in the 182-mm-ML neotype, the tubercles extend up for over one-third the length on all three pairs of dorsal arms.

As in *meleagroteuthis*, the tubercles on the mantle are fused basally forming a narrow bar with a series of protuberances; in the 17-mm-ML juvenile from off New Zealand, the protuberances numbered about 14; in the large neotype they are much more numerous, but too irregular to count. The tubercles on the arms, again as in *meleagroteuthis*, are more widely and independently set; in the small specimen from New Zealand there were 10 on arms I, 9 on II, and 7 on III, while in the large neotype there were approximately 17 + on I, 13 on II, and 9 on III. In the juveniles, the tubercles are very apparent, but in the large adult they are much less conspicuous and on the arms are often only detectable with the aid of a probe.

In 1948, Robson created a new genus, *Histiotauma*, for a small juvenile of 7.2 mm ML collected by the ARCTURUS just south of the Galapagos Islands. He gave it the new specific name *oceani*. A study of his description together with examination of the type-specimen (now unfortunately very hard, distorted, and unsuitable for detailed examination) in the British Museum leads me to believe that it could well be a young of *miranda*, sharing with *miranda* such characters as the tubercles on the dorsal three pairs of arms, five rows of photophores on the base of arms IV, and an overall concentration of photophores that is midway between that of *bonnellii* and that of *meleagroteuthis*. The original poor condition and small size of the specimen render meaningless Robson's remarks on the difference displayed by the suckers on the arms and the tentacular clubs.

Histioteuthis miranda shows a close affinity to *Histioteuthis meleagroteuthis* and appears to bridge a gap between *meleagroteuthis* and what might be called the more normal line of histioteuthid exemplified by *reversa*. Like *meleagroteuthis*, *miranda* possesses the rows of tubercles on the arms and mantle and the moderately deep inner web, but in the matter of the concentration of the photophores, it stands midway between the

two forms, having fewer and larger photophores than *meleagroteuthis*, but more and smaller photophores than *reversa*.

I have found only two other published records of *miranda* in the literature, those of Joyce Allan (1945) and R. K. Dell (1959). Allan's two specimens, the larger being 10 mm ML, are inadequately described and illustrated. The specimens could not be located but from what is given, they are definitely not of this species. I would not venture a guess as to their specific identity. Dr. Dell kindly loaned me one of the three BANZARE specimens which he had (1959) referred to *miranda*. It proved to be *Histioteuthis atlantica* (Hoyle) and is discussed in this paper under that species.

Distribution.—*H. miranda* is definitely known at present from only four specimens. Three were taken in the South Pacific Ocean (Berry's specimen from off Victoria, Australia, and two from waters in the vicinity of New Zealand), and one (SIO specimen) was taken in the North Pacific Ocean off Mindanao.

The record of Robson's juvenile, which I referred questionably to this species, would extend the known range of *miranda* into the eastern Pacific.

All were captured in the upper 730 meters of water in proximity to land areas.

Histioteuthis meleagroteuthis (Chun, 1910)

Figs. 6, b; 8, c; 26; 27

Meleagroteuthis hoylei Pfeffer, 1900: 170 (*nomen nudum*); 1908: 292; 1912: 291, pl. 22, figs. 1-8.—Joubin, 1905: 65; 1924: 63, pl. 11, figs. 1-2, pl. 12, figs. 1-5.—Adam, 1954: 155, fig. 24, pl. 1, fig. 1.—Pearcy, 1965: 262.

Calliteuthis meleagroteuthis Chun, 1910: 170.—G. Voss, 1963: 123, fig. 27, a-c.—Clarke, M. R., 1966: 199.

Meleagroteuthis separata Sasaki, 1915: 131, figs. 1-2; 1916: 103; 1929: 262, pl. 22, figs. 4-6.—Akimushkin, 1954a: 1183; 1954b: 665; 1955a: 112; 1955b: 1139.—Betesheva & Akimushkin, 1955: 89.—Akimushkin, 1957: 130, fig. 6d; 1963: 192.

Calliteuthis separata, Clarke, M. R., 1966: 200.

Histioteuthis meleagroteuthis (Chun), G. Voss, 1967: 75.

Material Examined.—NEOTYPE: 1 ♂, ML 48.2 mm, TUI Oceanographic Cruise, 35°45'S, 176°20'E, 21 July 1962, 549-686 meters, AUZ 057.13.

OTHER MATERIAL: 1 ♀, ML 65.0 mm, ALBATROSS Sta. D5444, off Atalaya Pt., Batag Island, east coast of Luzon, Philippines, 3 June 1909, 695 meters, USNM.—1 ♀, ML approx. 51 mm, MMF 9593, from stomach of *Aphanopus carbo*, Fish Market, Funchal, Madeira, 18 Sept. 1956.—1 ♂, ML 39.2 mm, DANA Sta. 1163 II, 12°59'N, 32°49'W, 7 Nov. 1921, mw 1000.—1 ♂, ML 38.0 mm, IKMT No. 42, 35°42'S, 24°10'E, 17-18 Nov. 1962, 500 meters, SAM A29738.—1 ♀, 1 sex ?, ML 25.5-14.0 mm, DANA Sta. 1171 III, 8°19'N, 44°35'W, 13 Nov. 1921, mw 600.—1 ♀, ML 25.0 mm, DANA Sta. 1342 VIII, 34°00'N, 70°01'W, 15 May 1922,

mw 300.—1 sex ?, ML approx. 24 mm, MMF 13994, from stomach of *Aphanopus* sp., Fish Market, Funchal, Madeira, May 1958.—1 ♂, ML 17+ mm, PILLSBURY Sta. 269, 0°10'S, 7°19'E, 18 May 1965, 2020 meters.—1 sex ?, ML 16.0 mm, DANA Sta. 4009 IX, 24°36.5'N, 17°27'W, 18 March 1930, mw 2500.—1 sex ?, ML 9.1 mm, DANA Sta. 3871 III, 3°59'S, 100°31.5'E, 25 Oct. 1929, mw 400.—1 sex ?, ML 9.0 mm, DANA Sta. 4017 VIII, 29°13'N, 14°12'W, 27 March 1930, mw 600.

Description.—Entire body firm, semigelatinous. *Mantle* conical; walls thick, tapering gently to blunt posterior tip; width slightly more than one-half length, greatest usually just posterior to anterior margin. Anteroventral margin beneath funnel only slightly excavated with blunt lateral angles; median anterodorsal margin produced to low obtuse angle; lateral anterodorsal margins slightly asymmetrically excavated, left side more emarginated than right, most apparent in larger specimens.

Midline of dorsal surface of mantle with row of small *tubercles* fused basally to form strong ridge on anterior two-thirds of mantle.

Fins transversely oval, length less than half the mantle length; width slightly more than half the mantle length. Posterior margin slightly overreaches posterior tip of mantle; median notch present.

Funnel supported by double bridle. *Locking apparatus* strong crescentic cartilaginous ridge on either mantle wall; elongate oval cartilage with deep, broad, median groove on either funnel wall. *Funnel organ* fleshy; dorsal member inverted V-shaped pad with papilla at anterior apex, unsculptured; ventral member, two large kidney-shaped pads. *Valve* semicircular.

Head large, about half as long as mantle, width greater than that of mantle; markedly asymmetrical with left eye about twice size of right. *Sinus* present in anterior margin of both eyelids. Single *nuchal fold* dorsal to *olfactory organ*.

Buccal membrane with seven lappets and seven supports. Support attachments as follows: middorsal or first support bifurcate through web to dorsal sides of arms I; second supports through web to dorsal side of II, or bifurcate to ventral side of I and dorsal side of II; third supports to ventral side of III; fourth supports to dorsal side of IV.

Inner web connecting arms I, II, and III moderate in depth, about 10-18 per cent of length of longest arms; deepest segment between arms I and II. *Outer web* not developed.

Arms long, approximately one to one and a half times length of mantle; about coequal, with no consistent order of arm lengths; IV usually the shortest. Arms stout at base, gradually taper to slender tips. Aboral surface of arms I, II, and III with median row of *tubercles* extending from near base to approximately midarm. Aboral surface of III with short, low *swimming keel* at approximately midlength; keel does not appear to

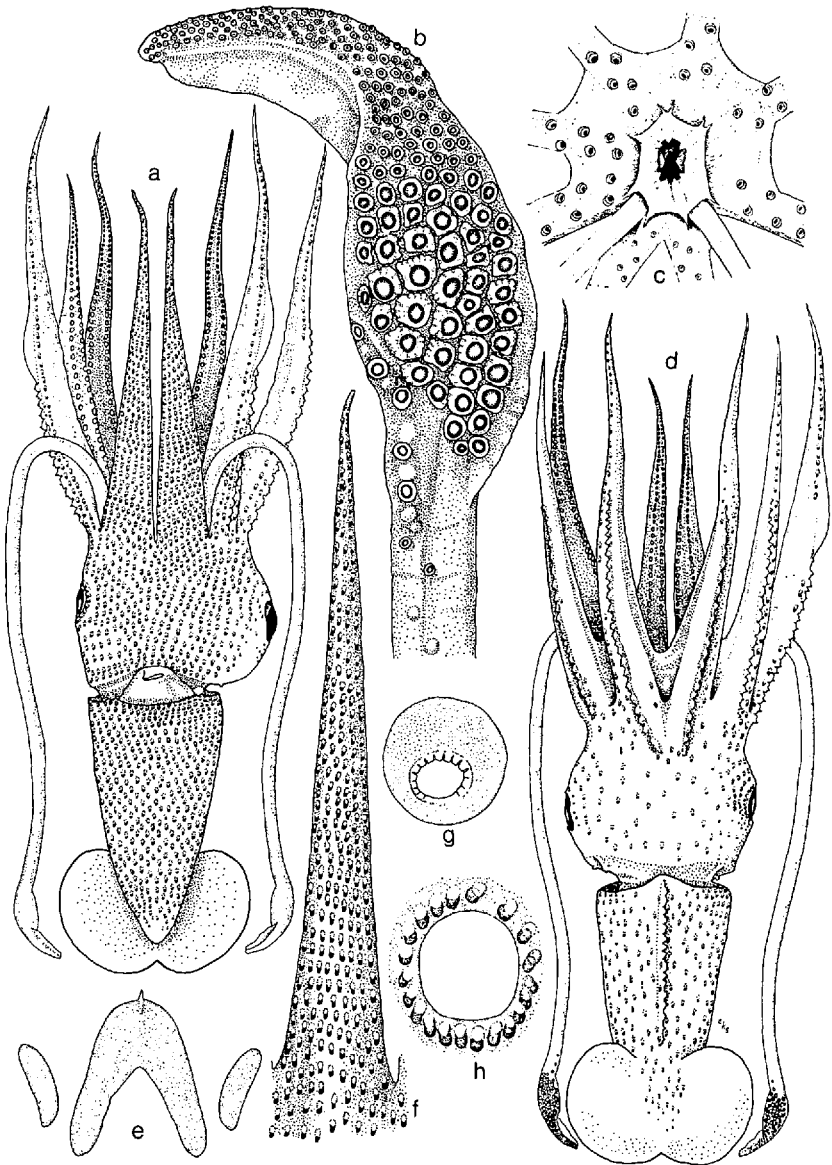


FIGURE 26. *Histioteuthis meleagroteuthis* (Chun, 1910): a, ventral view, neotype, AUZ 057.13, ML 48.2 mm; b, left tentacular club of same; c, buccal view of same; d, dorsal view of same; e, funnel organ of same; f, right arm IV of same; g, sucker, midarm II, *D* 1163 II, ML 39.2 mm; h, right eyelid of neotype.

continue to distal arm tip. No terminal keels apparent on arms I and II.

Oral surface of arms bordered on either side by low, fleshy *protective membrane*. Small globular, biserial *suckers* laterally set on short, delicate peduncles; suckers largest on base of arms, become progressively smaller as arm tapers; those on IV about one-third smaller than on other arms. Horny rings of suckers with about 6-20 low, square or round teeth on distal margin, proximal margin smooth or occasionally slightly indented. Basal suckers often with fewer and broader teeth.

First pair of arms of mature males *hectocotylized* in distal portion, with pedestals of suckers enlarged, producing a palisading effect to margin of arm; two rows of suckers throughout.

Tentacles long, slender, terminating in expanded club. *Club* with relatively broad manus and slender dactylus, orally bordered on either side by low *protective membrane*. Distal half of aboral surface of club with low, median *swimming keel*; no longitudinal *cleft* on proximal half.

Carpal adhesive apparatus on oral surface of tentacular stalk extends to about two club-lengths proximal to club. Proceeding toward club from distalmost point, arrangement on left tentacle of neotype as follows: in single series commencing on ventral margin of stalk 1 s, 2 pp, 2 ss, 2 pp, 2 ss; crossing over to dorsal margin, 2 pp, 2 ss, 2 pp set diagonally; then again in single row, 5 ss alternating singly with 4 pp extend up to base of manus and along its proximal dorsal margin.

Suckers on manus closely set in about six or seven rows. Suckers of central two or three rows appear to show only slight tendency for differential enlargement with growth of animal. As dactylus narrows, suckers decrease uniformly in size in increasingly shorter rows of five, four, and three. Horny rings of suckers of manus with about 25-30 triangular teeth on entire margin, with tendency for teeth on distal margin to be more elongate.

Photophores small, average approximately 1.0 mm long in 39.2-mm-ML specimen, 1.3 mm long in 48.2-mm-ML neotype; densely set. Those on ventral surface of mantle approximately uniform in size on anterior three-quarters, regularly diminish in size on posterior quarter. Photophores regularly spaced about one photophore length apart for entire length, absent only from extreme posterior tip of mantle. Approximately 40-45 photophores in entire anteromarginal row; with exception of scattered few, each heads a descending oblique row of organs. Approximately 25-27 photophores in diagonal row originating in vicinity of lateral angle on ventral surface.

Photophores on dorsal surface of mantle reduced in size and number, more widely set in less obvious pattern, extend to near posterior tip of mantle. No noticeable difference in density of photophores between right and left sides on either surface of mantle.

TABLE 10

MANTLE MEASUREMENTS (IN MM) AND INDICES OF *Histioteuthis meleagroteuthis* (CHUN, 1910)

	Neotype AUZ 057.13	D 1163 II	SAM A29738	D 1171 III	D 1342 VIII	D 4009 IX	D 1171 III	D 3971 III	D 4017 VIII
	♂	♂	♂	♀	♀	—	—	—	—
ML	48.2	39.2	38.0	25.5	25.0	16.0	14.0	9.1	9.0
MWI	50.4	56.1	56.6	42.4	52.0	50.0	57.8	68.2	64.5
HLI	58.7	69.0	55.3	60.8	58.0	49.5	48.2	66.0	46.7
HWI	65.3	50+	—	53.0	64.0	72.0	71.5	—	67.8
FLI	49.8	39.5	39.5	39.2	44.8	39.4	32.5	50.5	41.2
FWI	67.5	58.2	65.0	54.5	62.5	62.5	44.5	76.9	64.5
AI I	—	123.0	168.5	101.0	114.0	131.3	93.5	—	180.0
II	148.0	129.0	187.0	102.0	155.2	120.0	101.3	—	179.0
III	—	127.7	—	110.0	124.0	120.0	110.9	—	189.0
IV	133.2	120.0	158.0	80.4	96.0	93.7	103.6	—	156.6
TLI	238.0	170.0	273.0	137.3	176.0	148.0	205.0	273.0	239.0
CLI	33.6	27.6	32.3	23.9	31.6	31.2	31.4	44.0	41.2
M+I	12.5	12.8	13.7	9.3	13.6	18.8	12.9	22.0	14.5
IWI A	14.3	14.9	16.9	17.9	12.1	Trace	Trace		
B	14.3	18.4	17.6	14.3	11.9				
C	19.9	17.4	15.5	14.3	10.3				

Photophores on ventral surface of head as closely set in oblique rows as on ventral surface of mantle; due to asymmetric enlargement of left eye, photophores on that side more widely spaced. Circlet of 19-21 organs evenly set around margin of right eyelid.

Base of arm IV with 8-9 longitudinal rows of photophores, regularly decreased in number as arm narrows; only two remain on distal end of arm with only dorsalmost of these, originally a median row, extending to tip. Base of III with four longitudinal rows of photophores, two to either side of tubercular row; one ventral row extends to tip. Base of arms II and I appear to have three longitudinal rows of photophores, one dorsal and two ventral to tubercular row; one ventral row continues to distal tip.

Single set of *male genitalia* present, on left side. No *spermatophores* available.

Gladius delicate, translucent, strongly concave on ventral surface. Vane long, GVLI 75.2-77.0; moderately broad, GVWI 26.0-28.9 (two pens, 41.5 and 88.0 mm respectively); posterior lateral margins thickened, darkly pigmented; anterior lateral margins thin and colorless. Posterior

tip of gladii damaged. Larger gladius more darkly pigmented throughout than smaller one.

Upper beak with recessed false jaw angle. Lateral wall of lower beak with strong median ridge.

Radula of a specimen from North Atlantic illustrated. Laterals of increasing asymmetry and length, first to third. Small marginal plates present.

Neotype.—Auckland University, New Zealand, AUZ 057.13.

Neotype Locality.—South Pacific Ocean, 35°45'S, 176°20'E, 549-686 meters.

Discussion.—In 1900 Pfeffer erected the genus *Meleagroteuthis* for his new species of histioteuthid, *Meleagroteuthis hoylei*; the designation was unaccompanied by a description or illustration and hence a *nomen nudum*. But in 1908, he published an adequate description, and thereby established the name.

Chun, in 1910, submerged *Meleagroteuthis* as a subgenus of *Calliteuthis* and renamed Pfeffer's species *Calliteuthis meleagroteuthis*, since *Histiopsis hoylei* Goodrich, 1896, had prior claim on the specific name *hoylei*. Now with the genus *Calliteuthis* submerged, we have *Histioteuthis meleagroteuthis* (Chun) as the proper name for this species.

A species in the literature which confuses the picture of *H. meleagroteuthis* is *Meleagroteuthis separata* Sasaki, 1915, which differs only in the shape of the clubs and the arrangement of the tentacular suckers. I agree with G. Voss (1963) that the appearance of the clubs is obviously the result of mutilation and subsequent regeneration. Similar instances of such were found in two specimens of *Histioteuthis heteropsis* and are described in the discussion of that species. Thus, I consider Sasaki's species to be synonymous with *meleagroteuthis*. The only specimens in the literature known to me which have subsequently been identified as *separata* are those of Akimushkin (1954a, 1954b, 1955a, etc.) from waters east of Japan. In personal correspondence with Dr. Akimushkin, he described his material, obtained from the stomachs of whales, as specimens in exceedingly poor condition, lacking tentacles and beaks, hence of little or no value in the problem concerned.

Histioteuthis meleagroteuthis may be distinguished from all other known histioteuthids by the median row of cartilaginous tubercles on the dorsal surface of the mantle and on the dorsal three pairs of arms, together with the overall pattern of densely set, small photophores, and the seven-parted buccal membrane. A closely related species, *H. heteropsis*, has a seven-parted buccal membrane and a similar photophore pattern, but lacks the tubercles on the mantle and arms. Another closely related species known only from a single very imperfect specimen taken off southwest Africa

will be discussed later under that form; the six-parted buccal membrane of this latter specimen is distinctive.

I have been fortunate to have available for study 14 specimens of *meleagroteuthis* ranging in size from 9.0 to 65.0 mm ML, from the Atlantic, Pacific, and Indian oceans. For such a widely distributed species there is little variation, and any minor differences that occur among the specimens appear at present to be more attributable to individual variation than to geographic variation. The specimen from the Philippines is the same one described by G. Voss (1963). The female of 38 mm ML from the South African Museum was discussed by G. Voss (1967).

In the larger specimens, 25.0-65.0 mm ML, the tubercles on the mantle number approximately 16 to 25. In order to include this with Pfeffer's count of 30 tubercles for his holotype of 32 mm ML, the number of tubercles might be stated to range from approximately 16 to 30 in the size range considered. The 14.0- to 16.0-mm-ML specimens showed traces of only a few tubercles, while the smaller juveniles had no traces at all of the tubercles.

The tubercular row on arms I originates proximal to the base of the arm. Basally, the row on the left arm makes a sharp turn toward the median line of the head, apparently another case of asymmetry between the right and left sides. In the larger specimens, the number of tubercles ranged from 17 to 27. In the 16.0- and 14.0-mm-ML specimens, only a few tubercles on the base of the arm could be detected, deeply embedded beneath the skin.

The tubercular row begins progressively higher on the arms, proceeding from I to III, and occupies progressively less of the length of the arm. On II, the tubercles numbered 14-21 in the larger individuals, and there were only traces of a few on the base of the arm in the 16.0- and 14.0-mm-ML specimens. On III, there were 10-14 tubercles in the larger specimens, but no trace in the 16.0-mm-ML specimen and the smaller juveniles.

The tubercles on the arms differ from those on the dorsum of the mantle, in that they are triangular in shape and tend to remain separate, fusing only at the very base; whereas on the mantle the tubercles fuse into a solid cartilaginous ridge and are individually recognizable only as protruding knobs.

The inner web connecting the dorsal arms in the larger specimens exists as but a trace in the specimens of 16.0 mm ML and under. Even though these small specimens lack such important specific characters as the tubercles and web, they do possess, even as small as 9.0 mm ML, the pattern of densely set small photophores on the ventral surface of the mantle and head. However, the exact number of rows of photophores on the different arms is not apparent until a somewhat later stage.

A degree of variation is displayed in the attachments of the second

supports of the buccal membrane. In eight specimens with the buccal membrane intact, the second supports were both single to the dorsal side of II in three individuals; both bifurcate, to the ventral side of I and dorsal side of II, in two individuals; bifurcate, as described, on the left side, single, as described, on the right in two individuals; bifurcate, as described, on the right side, single, as described, on the left in one individual. In all cases, the attachment to II was the stronger.

Pfeffer's holotype of 33 mm ML was a unique specimen taken in Fonseca Bay on the west coast of Central America. It was deposited in the Hamburg Museum, the collections of which were destroyed during World War II. Since the type could not be located after much search, it must be presumed no longer extant, thus giving rise to the necessity of selecting a neotype for this species. I have selected the male of 48.2 mm ML from off New Zealand to fill this need. Like the holotype, it is from the Pacific Ocean, of the same approximate size, and compares well with Pfeffer's description. It is in excellent condition, except for the skin on the dorsal three pairs of arms, hence the incomplete pattern of photophores on the arms in the illustration.

Remarks.—The occurrence of *H. meleagroteuthis* in stomachs of sperm whales in the waters of the Kuril Islands, northwestern Pacific (Betesheva & Akimushkin, 1955, and Akimushkin, 1955b, reported as *Meleagroteuthis separata*) is evidence of a sizeable population of this species in this area.

Distribution.—*H. meleagroteuthis* is widely distributed in the North Atlantic south of about 35° latitude; in the South Atlantic, it occurs off the west and south coasts of Africa; in the North Pacific, it is widely distributed south of about 50° latitude; in the South Pacific, it has been taken north of New Zealand and in the Indian Ocean from west of Sumatra. The majority of the specimens were taken in waters adjacent to land.

Analysis of the data indicates that this species, collected by nets fishing to maximum depths of about 100 to 2020 meters, probably lives chiefly between about 100 to 700 meters.

***Histioteuthis bruuni*, n. sp.**

Figs. 3, i, j; 6, c; 27; 28

Material Examined.—HOLOTYPE: 1 ♂, ML 80 mm, DANA Sta. 3980 VI, 23°26'S, 3°56'E, 17 Feb. 1930, mw 6000.

Description.—Mantle conical; width slightly more than half of length; walls thick, firm, semigelatinous. Anteroventral margin beneath funnel only slightly excavated with blunt lateral angles; median anterodorsal margin produced into low, broad, obtuse angle. Continuous ridge of *tubercles* down dorsomedian line on anterior two-thirds of mantle.

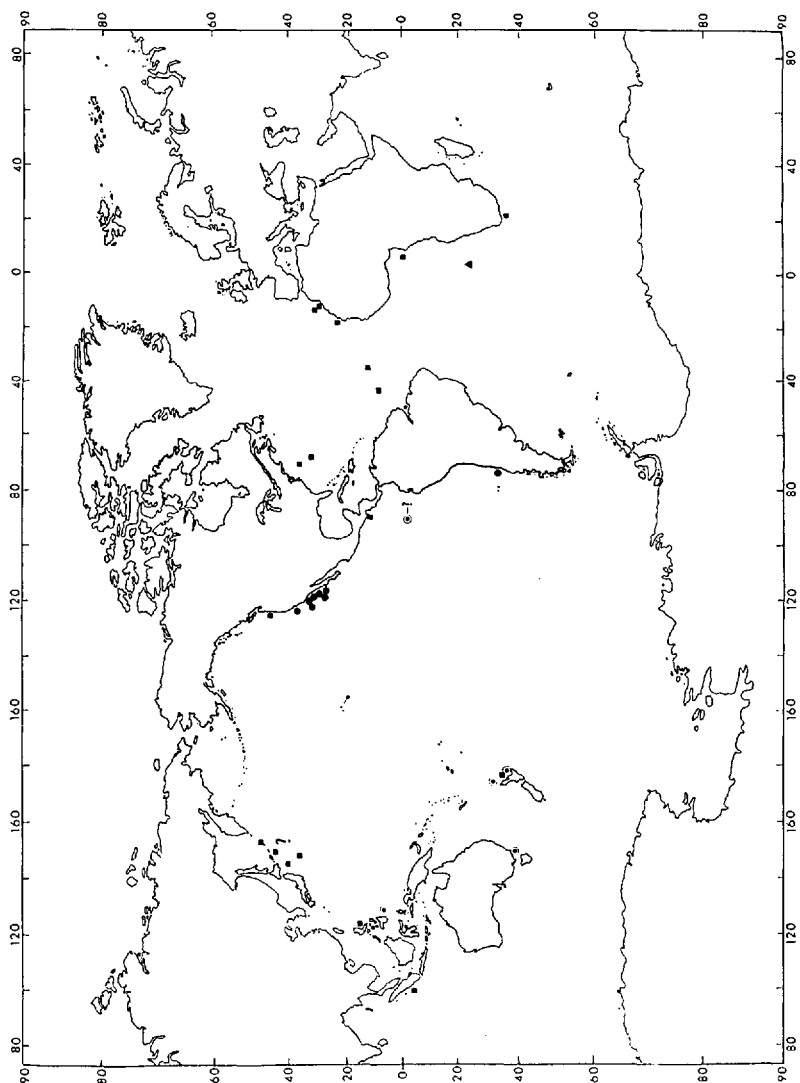


FIGURE 27. Distribution of confirmed, identified specimens. ● = *Histoteuthis heteropsis* (Berry); ○ = *H. miranda* (Berry); ■ = *H. melegrocephalus* (Chun); ▲ = *H. bruuni*, n. sp.

Fins partially destroyed; posterior margins free, extending beyond posterior tip of mantle.

Funnel with double bridle. *Locking apparatus*, a crescent-shaped ridge on mantle wall much heavier posteriorly than anteriorly; funnel cartilage broad with deep central groove. Dorsal pad of *funnel organ* typical inverted V-shaped with anterior apical papilla; arms fleshy, swollen but unsculptured; two ventral pads oval. *Valve*, large semicircular.

Head large, slightly exceeding mantle in width; asymmetrical with left eye about twice size of right.

Buccal membrane asymmetrical with six lappets and six supports. Support attachments as follows: first or middorsal bifurcate to dorsal sides of arms I; second left support to dorsal side of II, second right support bifurcate to ventral side of I and dorsal side of II, third right support to ventral side of III; fourth right support to dorsal side of IV; on left side, latter two supports and lappets from which they lead are, as it were, fused into one lappet with bifurcate attachment to ventral side of III and dorsal side of IV.

Inner web destroyed, but appears to have been moderate in depth (possibly 10-15 per cent length of longest arm).

Arms long, one to one and a half times length of mantle, stout basally, tapering to slender tips. Median line of aboral surface on I, II, and III with series of small separate *tubercles* extending from near base to slightly less than half the length of the arm. Two rows of small *suckers* on oral surface of arms, marginally set, largest basally; those on IV not noticeably smaller than those on other arms. Horny rings with about 13-17 small, round or square teeth on distal margin, proximal margin irregular to smooth.

Distal third to half of first arms *hectocotylized* with sucker pedestals enlarged giving a palisading effect on lateral view; suckers in two rows throughout.

Tentacles missing.

Photophores small, appear to have been densely set; approximately 20 in circlet around right eyelid.

Single set of *male genitalia*, on left side, with *spermatophores* (SpLI 0.023). Ejaculatory apparatus with single large median loop; relatively short cement body (CBI 18.3-25.2) with oral connective complex with high, thin collar and deep cavity. Inner tunic at aboral end of ejaculatory apparatus just oral to collar of cement body distinctly corrugated. Sperm mass (distorted by contraction) long (SpMI 36.6-41.4).

Gladius delicate, translucent, strongly concave ventrally with long vane (GVLI 76.0), moderately broad (GVWI 31.2).

Lower *beak* with strong median ridge on lateral wall.

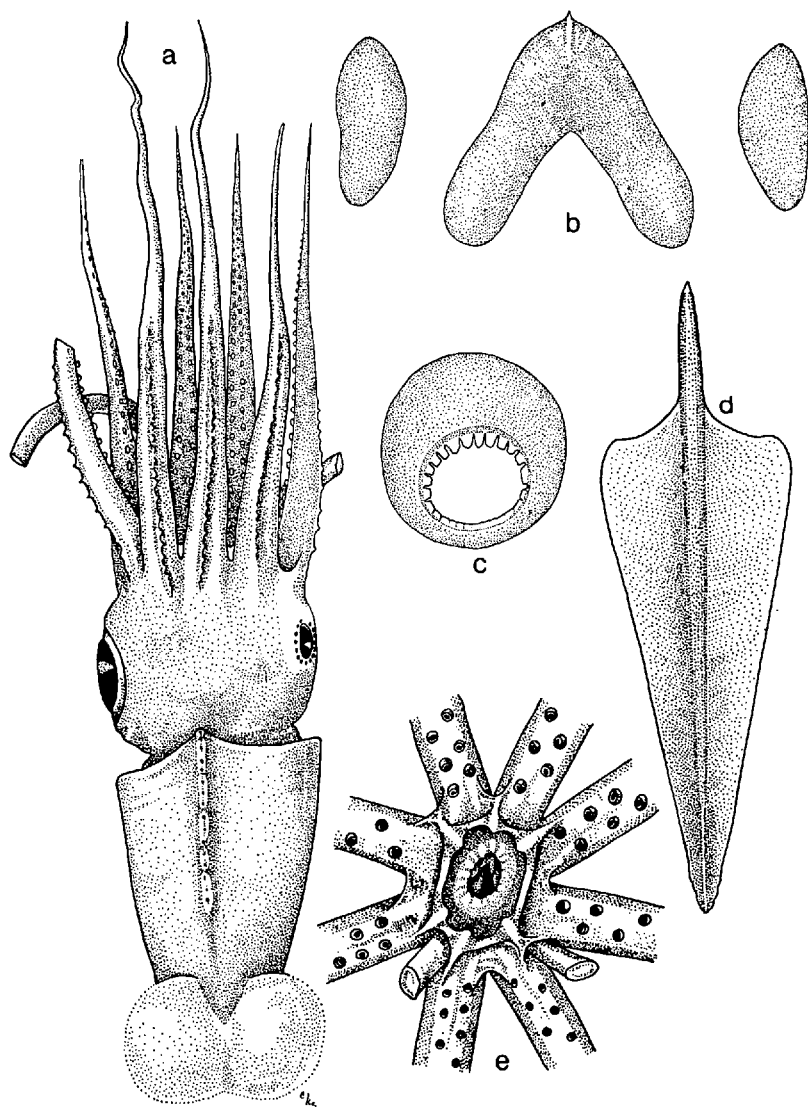


FIGURE 28. *Histioteuthis bruuni*, n. sp., holotype, ML 80 mm, D 3980 VI: a, dorsal view; b, funnel organ; c, sucker from 7th row, right arm II; d, gladius; e, buccal view.

TABLE 11
MANTLE MEASUREMENT (IN MM) AND INDICES OF HOLOTYPE
OF *Histioteuthis bruuni*, n. sp.

ML	80.0	FWI	56.0
MLI	32.2	AI I	147.5
MWI	55.0	II	122.5
HLI	46.3	III	127.0
HWI	—	IV	120.1
FLI	49.0	M+I	10.1

Type.—Zoologisk Museum, København.

Type-Locality.—South Atlantic off southwest Africa, 23°26'S, 3°56'E, mw 6000.

Discussion.—This lone specimen, a mature male, collected by the Danish DANA Expedition, 1928-30, from the South Atlantic off southwest Africa, is in very poor condition, completely denuded of skin, with tentacles missing, and with most of the suckers stripped from the arms. Its close relationship to *H. meleagroteuthis* is obvious, as they share such major characters as the tubercles on the arms and dorsum of the mantle and apparently the densely set, small photophores (indications of such around the margin of the right eyelid and the anterior margin of the mantle in *bruuni*). However, the two species differ strikingly, in that the buccal membrane in *bruuni* is six-membered rather than seven as in *meleagroteuthis*.

Since the above characters easily distinguish *bruuni* from all other histioteuthids, I do not hesitate to name it as new, despite the poor and incomplete condition of the unique specimen.

Remarks.—The specific name *bruuni* is in honor of Dr. Anton Fr. Bruun whose contributions to our knowledge of cephalopods and the sea in general are well known, and whose infectious enthusiasm for knowledge and for all people was an inspiration for all who met him. Dr. Bruun took part in the circumnavigation of the world by the DANA in 1928-30, on which expedition this specimen was collected.

Distribution.—This species is known at present only from the locality of the unique type-specimen, taken in the South Atlantic off southwest Africa with the net fishing to a maximum depth of approximately 3000 meters.

Histioteuthis heteropsis (Berry, 1913)

Figs. 1, a-c; 4, c-e; 6, d; 8, d; 27; 29; 30

Meleagroteuthis hoylei Pfeffer, Berry, 1912a: 305, text-figs. 13-16, pl. 50, figs. 1-3, pl. 51, pl. 52, figs. 5-7.

Calliteuthis (Meleagroteuthis) heteropsis Berry, 1913: 75.

Material Examined.—SYNTYPE: 1 sex ?, ML 51 mm, ALBATROSS Sta. 4544, Monterey Bay, California, 1323-1828 meters, USNM 5998.

OTHER MATERIAL: 1 ♂, ML 88.5 mm, AHF 8291-62, 33°27'N, 118°53'W, Nov. 1962.—1 ♂, ML 81.0 mm, AHF-D5693.—2 ♀♀, ML 71.5-22.2 mm, AHF 8934, 33°08'45"N, 118°33'15"W, 18 Sept. 1963, 485-492 meters.—1 ♀, ML 64.5 mm, AHF 8018, Catalina Basin.—2 ♀♀, ML 64.0-24.3 mm, AHF 9057-68, 33°26'45"N, 118°38'50"W, 14 Nov. 1963, 454-485 meters.—1 ♂, 3 sex ?, ML 60.1-15.0 mm, VELERO Sta. 8030, Catalina Basin, 9 Aug. 1962, 582 meters.—1 ♂, ML 50.4 mm, AHF 8716, 33°13'45"N, 118°41'40"W, June 1963, 414 meters.—2 ♂♂, 2 ♀♀, ML 43.5-22.2 mm, AHF 8935, 33°15'35"N, 118°45'38"W, 18 Sept. 1963, 394-424 meters.—4 ♀♀, 4 sex ?, ML 39.0 mm, VELERO Sta. 8025, Catalina Basin, 7 Aug. 1962, 528 meters.—1 ♀, 1 ♂, ML 36.3-25.3 mm, AHF 9249-64.—1 ♀, ML 34.7 mm, AHF 8347-63, 33°18'58"N, 118°46'40"W, 1282 meters.—3 ♀♀, 1 ♂, ML 33.5-16 mm, AHF 8114.—7 ♀♀, 2 ♂♂, ML 33.2-15.0 mm, VELERO Sta. 8028, Catalina Basin, 8 Aug. 1962, 655 meters.—2 ♀♀, 2 ♂♂, ML 32.6-14.2 mm, VELERO Sta. 8023.—1 ♀, ML 32.5 mm, AHF 2057-51, 33°21'34"N, 118°35'56"W, Sept. 1951, 803 meters.—1 ♀, 1 ♂, ML 32.3-18.7 mm, AHF 8963, 33°25'18"N, 118°40'08"W, 18 Oct. 1963, 262 meters.—1 ♂, ML 31.0 mm, ELTANIN Sta. 742-20, 33°33'S, 72°45'W, 26 Sept. 1963, 864 meters.—1 ♂, ML 30.0 mm, AHF 8432-63, 33°25'50"N, 118°46'00"W, Jan. 1963.—2 ♂, 3 ♀♀, 2 sex ?, ML 29.0-11.0 mm, AHF 8116.—2 ♀♀, 2 sex ?, ML 27.0-7.0 mm, VELERO Sta. 8027.—2 ♀♀, ML 26.5-22.1 mm, AHF 7221, Catalina Basin, 12 Sept. 1960, 585 meters.—2 ♂♂, ML 24.3-21.4 mm, AHF 7414.—1 ♀, ML 21.6 mm, AHF 8879, 32°54'44"N, 119°10'22"W, 27 Aug. 1963.—1 ♀, ML 21.3 mm, AHF 8243, 33°24'N, 118°40'W, Oct. 1962, 463-485 meters.—1 ♀, 1 ♂, ML 21.1-20.0 mm, AHF 8961, 33°21'27"N, 118°35'25"W, 18 Oct. 1963, 301-333 meters.—1 ♀, ML 20.8 mm, AHF 9167-63, 33°13'30"N, 118°37'05"W, 18 Dec. 1963, 182-197 meters.—1 ♀, ML 19.3 mm, AHF 8117, 33°22'47"N, 118°40'00"W, Aug. 1962.—1 ♀, 1 ♂, ML 19.7-18.2 mm, AHF 8788, 33°37'22"N, 117°58'16"W, June 1963, 258 meters.—1 spec., SIO-PAS 5406-13, 27°34'N, 119°31'W, 28 June 1954, 0-170 meters.—1 spec., SIO-B6212-120.45, 27°43'N, 115°33'W, 1 Dec. 1962.—1 spec., SIO-6204H, 33°09'N, 123°13'W, mw 2000.—1 spec., SIO-H50-287, 32°58'N, 118°23'W, 7 Dec. 1950, 1190 meters.—1 spec., SIO-trawl 1, San Diego trough, 3 Aug. 1954, 0-712 meters.—1 spec., SIO-trawl 5, 32°33'N, 117°27'W, 26 Aug. 1954, 535 meters.—3 spec., SIO-C6303-Cobb 58-6, 33°04'N, 121°58'W, 6 March 1963, 490 meters.—3 spec., SIO-C6303-Cobb 58-7, 32°07'N, 122°29'W, 6 Mar. 1963, 640 meters.—1 spec., SIO-C6303-Cobb 58-21, 31°00'N, 119°32'W, 19 March

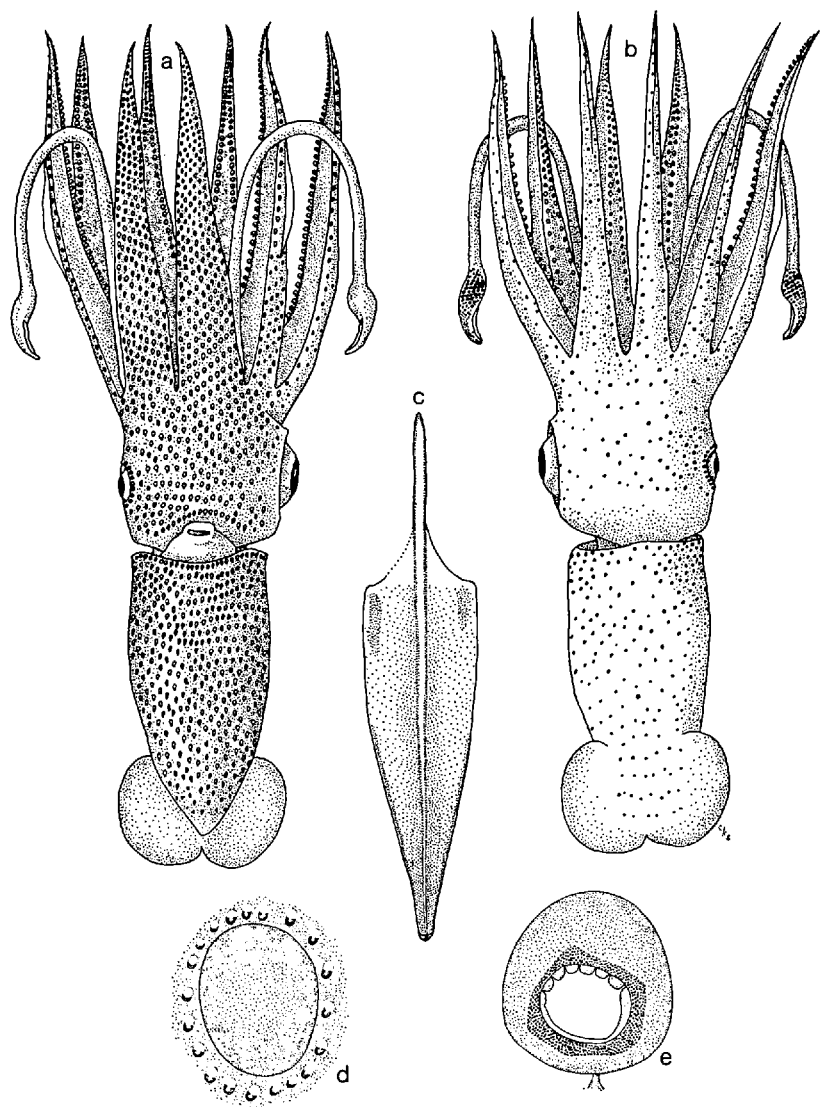


FIGURE 29. *Histioteuthis heteropsis* (Berry, 1913): a, ventral view, SIO-C6303 Cobb 58-6, ML 70.0 mm; b, dorsal view of same; c, gladius, SIO trawl 1, ML 74.5 mm; d, right eyelid, SIO-C6303 Cobb 58-6; e, sucker from 17th row, arm I of same.

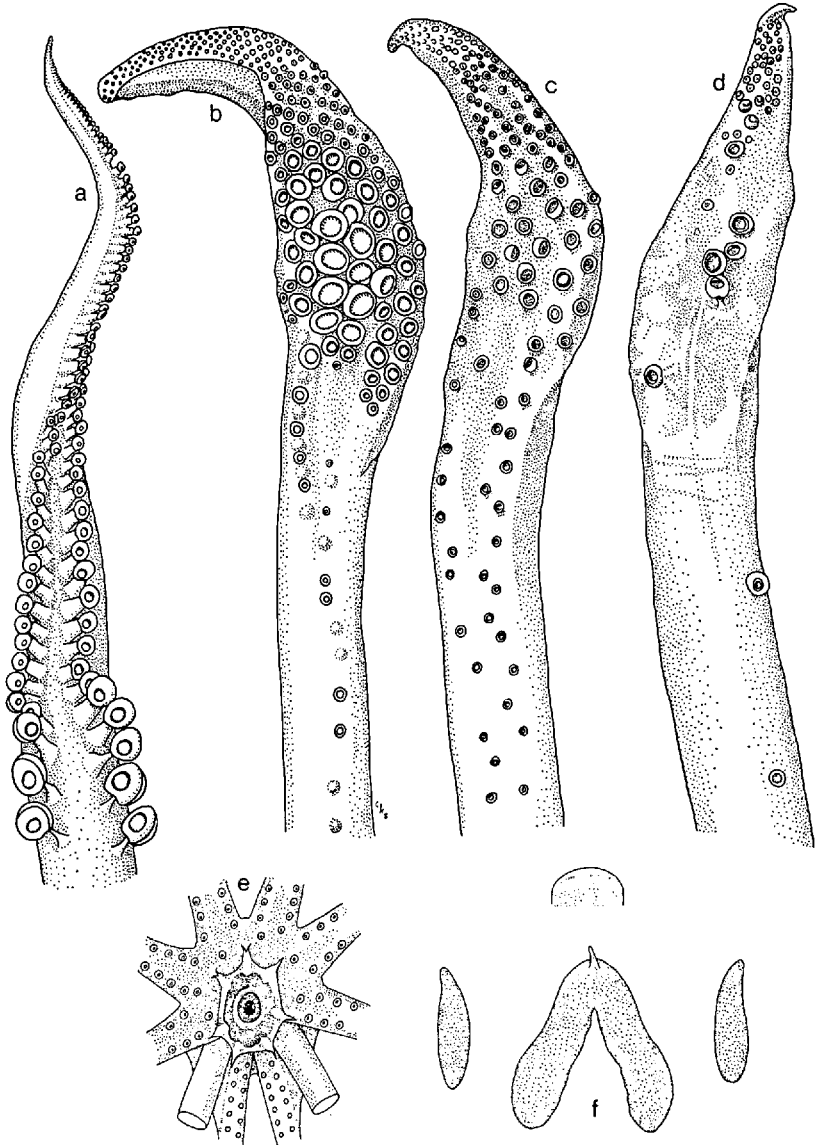


FIGURE 30. *Histioteuthis heteropsis* (Berry, 1913): a, left arm IV of male, SIO trawl 1, ML 74.5 mm; b, left tentacular club, SIO-C6303 Cobb 58-6, ML 70.0 mm; c, partially regenerated left tentacular club, V 8027, ML 25.5 mm; d, partially regenerated right tentacular club, V 8025, ML 29.3 mm; e, buccal view, SIO-C6303 Cobb 58-6; f, funnel organ and valve of same.

1963, 457 meters.—6 spec., SIO-C6303-Cobb 58-27, 29°12'N, 118°09'W, 23 Mar. 1963, 457 meters.

Description.—*Body* firm, semigelatinous, thick walled. Anterior half of conical mantle with almost parallel sides, posterior half tapers to blunt tip; width approximately half mantle length. Anteroventral margin with only slight excavation beneath funnel, low, blunt, lateral angles; mid-anterdorsal margin produced into low obtuse angle. No median ridge of *tubercles* on dorsum.

Fins transversely oval in outline, less than half mantle in length; slightly more than half mantle in width. Posterior margin of lobes slightly exceed tip of mantle; median notch present.

Funnel strong, with double bridle. Typical histioteuthid *locking apparatus* heavy, well developed. *Funnel organ* fleshy, unsculptured; dorsal member, inverted V-shaped pad with long arms and well-developed papilla at anterior apex; ventral member, two elongate oval pads. *Valve* well developed, semicircular.

Head large, slightly wider than mantle, strongly asymmetrical; left eye more than twice size of right. *Olfactory organ*, a fleshy papilla. No *nuchal folds* apparent.

Buccal membrane seven-membered with attachments as follows: first or middorsal support bifurcate through web to dorsal side of arms I; second supports through web to dorsal side of II, or bifurcate through web to ventral side of I and dorsal side of II; third supports to ventral side of III; fourth supports to dorsal side of IV.

Moderate *inner web* connecting dorsal three pairs of arms, approximately 11-23 per cent of longest arm; *outer web* slightly less developed, with resultant deep pocket between arms and webs.

Arms strong, stout basally, tapering distally to delicate tips; approximately one to one and a quarter times length of mantle, about subequal, but I and IV usually slightly shorter; approximate arm formula $2 = 3.1.4$. *Swimming keel* at midlength of III runs distance equal to about one-quarter the length of arm, then diminishes to low median keel to tip of arm; dorsal two pairs of arms with low median *keels* on distal half. No median ridge of *tubercles* on arms.

Two rows of *suckers* on arms widely separated, each row following outer margin of arm. Short peduncle of suckers rises from fleshy base, which is continuous on outer margin with low fleshy *protective membrane*; suckers approximately uniform in size to distal quarter. *Horny rings* of larger suckers toothed with 5-15 low, often poorly defined, round or square teeth on distal margin; rings of smaller distal suckers more toothed, often around entire margin; denticulate collar narrow.

Distal third to one-half of both dorsal arms *hectocotylized* in larger

males (noted in males 50.4 mm ML and over); suckers remain in two rows.

Tentacles long, terminating in expanded clubs. Aboral surface of *club* with strong swimming keel on distal half; no cleft in proximal half. Low *protective membrane* along either margin of oral surface of club. *Suckers* of manus and dactylus closely and regularly set; on manus in rows of six to eight, with suckers of central rows slightly enlarged; rows on dactylus decrease to four. *Horny rings* of larger suckers of manus with entire margins denticulate, with approximately 30-34 small, pointed or blunt teeth having tendency to be more pronounced on distal margin.

Carpal arrangement on tentacular stalk extends about two to two and one-half times the length of club, proximal to club. From distalmost point from club, uniserial arrangement as follows: single small suckers (1 s), then 2 pp, 2 ss, 2 pp, 2 ss, 2 pp (with decreasing intervening space) along ventral margin of stalk, crossing over to dorsal margin, arrangement continues with 2 ss and 2 pp diagonally set in double row, followed by 2 ss almost opposite each other; then uniserially again 1 p, 1 s, 1 p, 1 s, 1 p to base of manus, followed by a usually enlarged sucker (1 s), then 1 p, 1 s, 1 p, 1 s up the dorsal margin of manus. Above arrangement most consistent, occurring on either tentacle.

Photophores on ventral surface of mantle small (in 63.0-mm-ML specimens, average photophore approximately 1.5 mm long, 0.7 mm wide), densely set, about one photophore distance apart on anterior three-quarters. Photophores of diminishing size and greater distance apart on posterior quarter. Approximately 19-22 organs in diagonal row on ventral surface, originating near lateral angle. On dorsal surface of mantle, photophores fewer, smaller, more widely, but still regularly spaced to near posterior tip.

Photophores on ventral surface of head of same size and density as on ventral surface of mantle; due to asymmetry of eyes, organs on left side more widely spaced. Circlet of usually 19-20 photophores around margin of right eyelid; irregular circlet of widely spaced smaller organs around margin of left eyelid; remainder of photophores on head in diagonal rows.

Eight to nine rows of photophores on base of arms IV, decreasing regularly to two distally, dorsalmost of which extends to tip. Base of arms III and II with four rows of photophores, but only three rows extending to any extent; ventral row continues to tip. Base of arm I with three to four rows of photophores; ventral row extends to tip.

Male genitalia single, on left side. Mature *spermatophores* found in four males, 54.6 to 88.5 mm ML. Spermatophores 1.80 to 2.76 mm long (SpLI 0.024-0.034), with short sperm mass (SpMI 10.9-16.6). Cement body long (CBI 55.5-63.6), with oral connective complex with ejaculatory tube. Connective complex with high thin collar and deep cavity; collar and immediate membranes of ejaculatory apparatus with distinct cor-

rugated appearance; complex separated from remainder of cement body by narrow neck.

Gladius delicate, ventral surface strongly concave. Vane long, 75.3-78.6 per cent of length of gladius; moderately broad, 25.7-21.9 per cent of length of gladius in gladii measuring 71.5 mm (♀ spec.) and 89.3 mm (♂ spec.), respectively; whole very lightly pigmented except for margins of rhachis; posteriorly tapering margins of vane slightly thickened.

Lower beak with strong median ridge on lateral wall.

Radula with weak, tear-shaped marginal plates. First lateral quite similar to rhachidian in shape, second lateral more asymmetrical, third lateral long saber-shaped.

Type.—Described from three syntypes; one deposited in United States National Museum, USNM 5998.

Type-Locality.—Monterey Bay and off Santa Barbara Island, California, United States, from 590-1829 meters.

Discussion.—*Histioteuthis heteropsis* was described by Berry (1913) after he at first (1912a) mistakenly referred the three original specimens to *Meleagroteuthis hoylei* (= *Histioteuthis meleagroteuthis*) because of lack of literature. After having access to Pfeffer's more detailed description and illustrations of *hoylei* in his 1912 monograph, Berry realized that the material represented a new species clearly distinguishable from *hoylei* by its lack of tubercular rows on the arms and mantle. Since Berry did not designate a holotype, the three original specimens must be considered syntypes. The one deposited in the U. S. National Museum was examined and was found to have been permitted to dry up sometime in the past. Subsequently placed in alcohol, it is now valueless for purposes of identification. I do not know the whereabouts of the other two syntypes, but fortunately Berry's 1912 description and illustrations are thorough, thereby establishing the species unquestionably.

Histioteuthis heteropsis shares with *H. meleagroteuthis*, and possibly the new species *Histioteuthis bruuni*, the character of the densely set, small photophores which distinguishes them from the other members of the family. *H. heteropsis* can be distinguished from its above-cited fellows by the lack of the tubercular rows. A problem arises in separating the juveniles that are below about 14 mm ML in size when, at least in the material available, no traces of the developing tubercles can be seen in *meleagroteuthis*. The only character that I have found, though admittedly not the best, is the additional carpal elements found in *heteropsis*.

Two female specimens exhibited cases of mutilation and subsequent regeneration of the club and tentacle. This is worthy of description, in light of the earlier discussion of *Meleagroteuthis separata* Sasaki and its relationship with *H. meleagroteuthis* (Chun). One, a specimen of 25.5 mm ML, which exhibited varying degrees of regeneration of several of

TABLE 12
MANTLE MEASUREMENTS (IN MM) AND INDICES OF *Histioteuthis heteropsis* (BERRY, 1913)

	SIO-C6303 Cobb58-7 ♀	AHF 8291 ♂	AHF 8934 ♀	AHF 9057-68 ♀	V 8030 ♂	V 8025 ♀	AHF 9249-64 ♀	Elt 742-20 ♂	AHF 9249-64 ♂	AHF 8934 ♀	AHF 8030 —
ML	132.0	88.5	71.5	64.0	60.1	39.0	36.3	31.0	25.3	22.2	15.0
MWI	45.8	52.0	49.0	48.5	50.2	59.0	52.3	54.8	60.5	57.6	64.0
HLI	31.3	53.2	61.5	50.3	51.4	49.5	49.5	53.2	50.5	46.3	53.4
HWI	—	50.2	—	56.0	51.2	67.5	60.5	69.3	75.0	69.0	65.4
FLI	26.5	—	38.6	—	34.9	33.6	40.2	33.5	42.3	37.4	42.7
FWI	50.0	—	56.0	—	48.2	—	58.1	54.2	62.5	55.8	60.7
AI I	103.0	101.0	125.6	106.8	123.5	101.4	104.0	90.4	107.0	101.3	93.3
II	106.0	101.0	125.6	113.1	133.0	114.7	110.1	100.0	102.9	103.6	106.8
III	107.6	101.9	125.6	115.7	128.8	110.2	102.0	90.4	107.0	108.0	106.8
IV	92.5	94.3	113.3	106.0	119.4	91.3	93.0	84.8	95.6	99.0	95.3
TLI	—	207.5	—	154.9	168.5	174.3	95.9	126.0	—	122.7	122.0
CLI	—	24.9	—	25.8	33.3	30.0	24.8	26.8	27.7	28.4	33.3
M+I	12.1	—	—	7.2	—	—	10.7	4.8	12.5	13.5	13.3
IWI A	15.5	22.0	17.8	18.5	11.0	17.9	21.5	20.4	15.2	16.7	—
B	16.9	23.6	17.8	20.0	—	15.7	17.5	23.6	14.8	15.8	—
C	16.2	20.0	21.2	17.6	10.5	19.7	17.5	21.8	18.2	15.8	—

the arms and had the right club missing, had an unusual regeneration of the left club (Fig. 30, c). The club was only slightly expanded and only about one-sixth its expected size. There was no swimming keel on the aboral surface and, on the oral surface, a much reduced number of suckers in approximately five irregular rows. Two irregular rows of suckers extended down approximately one-third the length of the tentacular stalk, one to either margin. All the suckers were approximately coequal in size, and no pads were apparent. The other specimen (29.3 mm ML), which was otherwise normal, had obviously suffered mutilation of its right tentacle (Fig. 30, d). The mended club was only slightly expanded, bore no swimming keel, and had only a few somewhat enlarged suckers sporadically set on the manus-appearing portion, followed by a small tight cluster of minute suckers on the terminal attenuate section. There were only two widely set suckers on the tentacular stalk.

Considerable variation appears to occur in the number of photophores in the different regional patterns in *heteropsis*. One example is in the number of photophores in the circlet around the margin of the right eyelid. In 59 specimens examined, there were 17 photophores in the circlet in two specimens, 18 in six specimens, 19 in 32 specimens, 20 in 18 specimens, and 21 in one specimen.

All four males that contained mature spermatophores were taken off the coast of southern California. The four lots of spermatophores were almost identical in appearance except for that from the 81.0-mm specimen (D5693). The spermatophores in this lot had a constriction in the cement body a short distance aboral to the connective complex, a noticeably larger loop in the ejaculatory apparatus, and a slightly different folding of the inner tunic on the oral shoulders of the cement body.

Distribution.—This species is so far known only from the North Pacific off California, and from the South Pacific off Valparaiso, Chile.

It is the commonest histioteuthid taken off California in the vicinity of the Catalina and San Pedro Basins. In his intensive study of the cephalopod fauna of these basins, Young (in manuscript) found that *heteropsis* undergoes a regular diurnal vertical migration, concentrating in the upper 400 meters at nighttime and in about 400 to 800 meters at daytime.

Though data concerning the additional specimens included in this study are inadequate for the study of vertical migration, they do confirm that the species lives chiefly in the upper 800 meters, with perhaps some scattering to depths of 1200 to 1300 meters.

Histioteuthis atlantica (Hoyle, 1885)

Figs. 3, k; 6, e; 8, e; 31-33

Histiopsis atlantica Hoyle, 1885a: 273 (*nomen nudum*); 1885b: 201; 1885c: 306; 1886: 180, pl. 30, figs. 9-15.

Histioteuthis cookiana Dell, 1951: 1 (in part: holotype and four of the paratypes designated as "short-webbed" series), figs. 4-5; 1952: 119, pls. 26-28.

Calliteuthis miranda Berry, Dell, 1959: 100 (in part: 34.0-mm-ML ♂; possibly the two remaining unexamined specimens).

Material Examined.—HOLOTYPE: 1 ♂, ML 35 mm, CHALLENGER Sta. 333, 35°36'S, 21°12'W, 13 Mar. 1876, 3710 meters, BM 1890.1.24.18.

HOLOTYPE OF *Histioteuthis cookiana* DELL: 1 ♀, ML 91 mm, coll. A. C. Kaberry, Cook Strait, 28 Nov. 1944, DMNZ-M5628.

OTHER MATERIAL: 1 ♀, ML 63.0 mm, coll. R. Greco, from grouper stomach, Cook Strait, 27 June 1956, DMNZ-M9830.—1 ♂, ML 53.0 mm, ELTANIN Sta. 1706, 43°45'S, 174°07'W, 22 May 1966, 250-275 meters.—1 ♂, ML 51.0 mm, DANA Sta. 3975 VI, 35°42'S, 18°37'E, 31 Jan. 1930, mw 1000.—1 ♂, ML 40.0 mm, A. BRUUN Cr. 6, Sta. 353A-7331, 38°15'S, 64°45'E, 2 July 1964, 350-2394 meters, IKMT.—1 ♂, ML 39.2 mm, ELTANIN Sta. 1405, 44°13'S, 162°06'E, 3-4 Feb. 1965, 200 meters.—1 ♂, ML 34.0 mm, BANZARE Sta. 71, 51°59'S, 98°59'E, mw 1200 (*Calliteuthis miranda* Berry, Dell, 1959).—1 ♂, 1 ♀, ML 33.5-32.0 mm, ELTANIN Sta. 97-14, 46°15'S, 76°18'W, 10-11 July 1962, 1830 meters.—1 ♂, 1 ♀, ML 25.5-22.0 mm, ELTANIN Sta. 165-15, 47°03'S, 76°17'W, 24 Aug. 1963, approx. 732 meters.—1 ♀, ML 25.0 mm, ELTANIN Sta. 326-20, 38°09'S, 74°31'W, 25 Nov. 1962, 1691-2072 meters.—1 ♂, ML 24.0 mm, TUI Oceanographic Cruise, 35°45'S, 176°20'E, 21 July 1962, 548-686 meters, AUZ 057.02.—1 ♀, ML 24.0 mm, ELTANIN Sta. 1402, 38°55'S, 179°27'W, 30 Nov.—1 Dec. 1964, 2178-2489 meters.—1 ♀, ML 23.5 mm, ELTANIN Sta. 1704, 43°50'S, 174°27'W, 22 May 1966, 725-800 meters.—1 ♂, ML 19.4 mm, ELTANIN Sta. 1692, 49°00'S, 161°57'W, 17 May 1966, 0-2300 meters.—1 ♀, ML 19.0 mm, GALATHEA Sta. 607, 44°18'S, 166°46'E, 17 Jan. 1952, mw 6600.—1 ♀, 1 sex ?, ML 18.3-14 mm, ELTANIN Sta. 1830, 42°00'S, 160°11'E, 8 Dec. 1966, 700-800 meters.—1 ♂, ML 17.0 mm, ELTANIN Sta. 1821, 40°07'S, 161°08'E, 4 Dec. 1966, 2500-3150 meters.—3 sex ?, ML 16+ to 7.0 mm, ELTANIN Sta. 1817, 40°07'S, 168°05'E, 2 Dec. 1966, 375-405 meters.—1 sex ?, ML 15.0 mm, ELTANIN Sta. 1835, 45°19'S, 160°11'E, 11 Dec. 1966, 1250-1375 meters.—1 ♀, ML 15.0 mm, TUI Oceanographic Cruise, between the Kermadec Islands and New Zealand, 1 Aug. 1962, 914-1052 meters, AUZ 119.05.—1 sex ?, ML 14.0 mm, ELTANIN Sta. 1823, 40°03'S, 160°41'E, 4 Dec. 1966, 46-52 meters.—1 sex ?, ML 12.8 mm, ELTANIN Sta. 1836, 45°29'S, 160°12'E, 11 Dec. 1966, 2030-2181 meters.

Description.—*Mantle* conical, of moderate length with greatest width usually at flared-out anterior margin; side gently tapering to blunt posterior point. Ventrally, anterior margin slightly excavated between lateral angles;

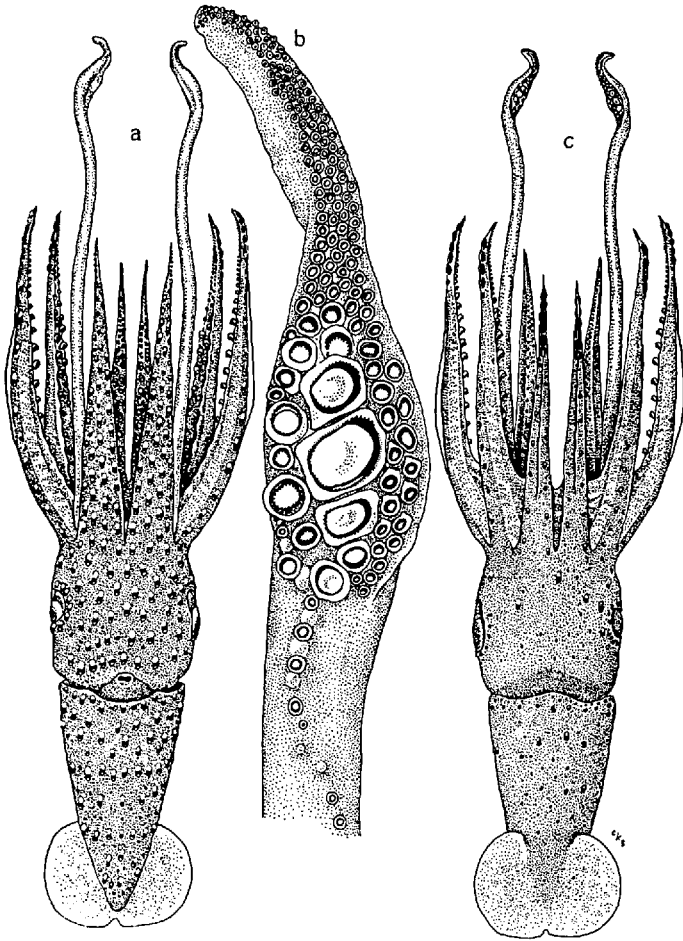


FIGURE 31. *Histioteuthis atlantica* (Hoyle, 1885), *Elt* 1706, ML 53.0 mm: a, ventral view; b, left tentacular club; c, dorsal view.

median anterodorsal margin forming a broad obtuse angle. Mantle walls relatively thick.

Fins delicate, transversely oval, projecting beyond posterior tip of mantle; united with a median notch; length approximately 30-47 per cent of ML; width approximately 55-65 per cent of ML (specimens 32.0-91.0 mm ML).

Funnel well developed with two dorsal supports. Mantle member of funnel-mantle locking apparatus strong, slightly crescent-shaped ridge,

narrow anteriorly, becoming heavy and fleshy posteriorly. Oval funnel cartilage with deep median groove. Dorsal pad of *funnel organ* with anterior apical papilla, broad shoulders, and short arms; two ridges, one leading to each arm, originating independently just posterior to papilla; at first narrow, then broad and swollen, and finally merging into swollen posterior lobes of arm. Two large oval ventral pads. *Valve* large, semicircular.

Head large, exceeding mantle in width. Typical histioteuthid disparity in size of eyes; left eye and eyelid about twice size of right; sinus present in anterior margin of eyelids. Single *nuchal fold* present anterior to small *olfactory organ*.

Buccal membrane with seven lappets and seven supports. Attachments to supports are as follows: middorsal or first support bifurcate to the dorsal sides of I, second supports to dorsal sides of II, third supports to ventral sides of III, and fourth supports to dorsal sides of IV.

First three pairs of arms connected basally by moderately deep *inner web* measuring about 17-30 per cent of longest arm; *outer web* only slightly developed.

Arms heavy basally, tapering to slender tips; length one to two times mantle length; length formula approximately 3.2.4.1. *Swimming keel* on III commencing just proximal of midarm; expanded for about one-third its length, then reduced to ridge to tip of arm. Low median keel on distal three-quarters of arms I and II. *Protective membrane* on either side of oral surface of arms low and fleshy.

Suckers relatively small, marginally set; those on IV only about one-half to one-third size on other arms; those on I, II, and III largest on distal third quarter, then abruptly becoming minute to tip of arm. Short stalks of suckers rising from fleshy pedestals. *Horny rings* of suckers on arms I, II, and III varying from almost smooth to 5-10 low teeth on distal and occasionally on entire margin. Horny rings of suckers on IV with more numerous, small, square teeth on distal or entire margin.

Tentacles long, slender, about one and one-half to three times mantle length. *Club* with expanded manus and moderately long, slender dactylus. Aborally, low swimming keel on dactylus; deep longitudinal *cleft* on dorsal side of manus.

Carpal adhesive apparatus beginning at about two to two and a half club-lengths proximal to club on oral surface of tentacular stalk. Most common carpal arrangement as follows: on stalk, uniserial row commencing on ventral margin with 2 ss and 2 pp widely set, followed by 2 ss, 2 pp, 2 ss, and 2 pp with decreasing intervening space. Row continuing with 2 ss, 2 pp, 2 ss somewhat diagonally set, then medially with 1 p, 1 s, 1 p, 1 s, 1 p, 1s, 1 p, to base of manus where next carpal sucker is much enlarged (slightly more than double size of preceding suckers in small specimens, and three to four times enlarged in the larger specimens of

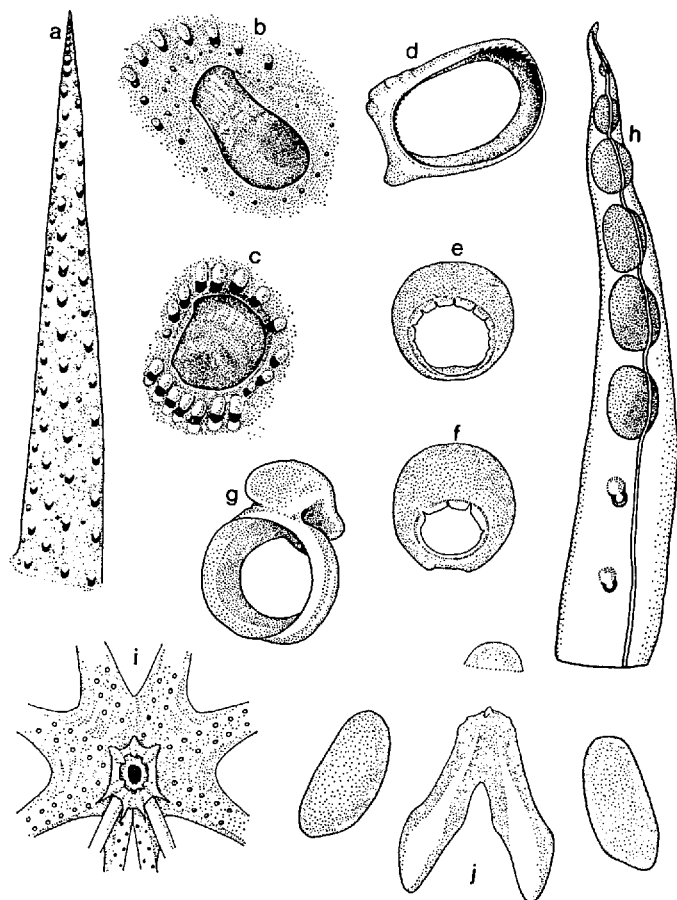


FIGURE 32. *Histioteuthis atlantica* (Hoyle, 1885): a, right arm IV, *Elt* 1706, ML 53.0 mm; b, left eyelid of same; c, right eyelid of same; d, largest tentacular sucker of same; e, sucker from 2nd row, arm II of same; f, sucker from 7th row, arm II of same; g, ring of large carpal sucker at base of manus, showing accessory growth, *D* 3975 VI, ML 51.0 mm; h, distal portion of arm I, showing terminal group of enlarged photophores, BANZARE 71, ML 34.0 mm; i, buccal view, *Elt* 1706; j, funnel organ and valve, BANZARE 71.

51.0-91.0 mm ML). Carpal arrangement continuing up dorsal margin of manus with 1 p, 1 s, 1 p, and 1 s.

Suckers on manus in about six rows, which narrow to five and four on slender dactylus. Median row on manus with four central, unequally enlarged suckers; first two (actually suckers number two and three in

TABLE 13
MANTLE MEASUREMENTS (IN MM) AND INDICES OF *Histioteuthis atlantica* (HOYLE, 1885)

* DMNZ M5628 ♀	DMNZ M9830 ♀	Elt 1706 ♂	D 3975 VI ♂	** Chal BANZARE		*** 71		Elt 97 ♀	Elt 97 ♂	Elt 326 ♀	AUZ 057.02 ♂	AUZ 119.05 ♀
				333 ♂	71 ♂	333 ♂	71 ♂					
ML	91.0	63.0	53.0	51.0	35.0	34.0	33.5	32.0	25.0	24.0	15.0	
MLI	—	—	31.9	37.0	36.5	39.1	36.4	33.0	—	—	—	—
MWI	46.2	53.2	58.8	55.3	62.8	52.9	48.0	53.0	56.4	58.3	—	—
HLI	—	24.5	59.5	43.2	—	44.1	53.2	55.3	42.7	—	—	—
HWI	—	—	65.5	55.3	—	—	67.5	—	64.0	—	—	—
FFLI	33.0	24.5	47.2	31.4	42.8	36.2	40.8	40.6	46.0	48.3	60.0	—
FWI	(52.9)	60.5	65.0	55.0	60.0	58.8	57.0	65.5	64.0	78.7	—	—
AI I	164.9	134.0	115.1	104.7	128.6	88.2	101.0	103.0	83.0	108.8	94.0	—
II	197.8	163.5	141.5	123 (approx.)	145.6	109.5	120.0	123.5	105.0	116.9	106.9	—
III	209.0	176.4	141.0	123 (approx.)	157.2	109.5	122.3	128.0	100.0	113.3	100.0	—
IV	175.9	150.5	127.0	—	143.0	97.0	113.4	116.0	88.0	108.3	88.6	—
TLI	407.0	298.0	237.8	308.0	—	140.4	212.0	269.0	335.0	—	—	—
CLI	(54.9)	38.4	34.0	51.6	—	29.4	33.1	33.0	24.0	—	38.0	—
M+I	—	11.9	11.3	6.3	—	9.1	7.8	10.3	17.6	16.7	16.7	—
IWI A	13.2	18.3	17.3	10.5+	—	26.1	20.3	17.1	21.8	17.9	—	—
B	(13.7)	29.0	22.7	—	—	29.5	22.4	22.0	23.6	23.9	—	—
C	(13.7)	29.8	28.0	12.8+	—	31.2	25.3	22.0	26.0	25.0	—	—

* Holotype of *Histioteuthis cookiana* Dell, 1951; indices from original measurements of Dell (1952: 119), except where in parentheses.

** Holotype, indices from original measurements of Hoyle (1885a: 180).

*** One of three specimens identified as *Calliteuthis miranda* Berry, by Dell (1959: 100).

row) usually with six to eight heavy teeth on proximal margin of ring, distal margins smooth or very finely toothed; next sucker (largest on club) and following sucker with irregular margins, partly smooth and partly cut into numerous irregular teeth. Dentition of above enlarged suckers less diverse in small specimens. Some suckers of ventral row with enlarged teeth on proximal margin. Remaining suckers of manus with small, pointed, triangular teeth on entire margin of rings. *Protective membrane* on either side of manus reduced as dactylus narrows.

Ventral surface of mantle with numerous intermixed large and small *photophores* in diagonal rows to near the posterior tip. Large organs in about six diagonal rows. Dorsal surface of mantle with fewer *photophores*. Ventral surface of head with *photophores* of intermixed sizes; numerous large ones in diagonal rows, except for immediately around eyelids. Eighteen *photophores* (17 large and one small) in circlet around right eyelid; about 12 to 16 small *photophores* in broken circlet around immediate margin of left eyelid in addition to typical arc of seven large *photophores* over anterior margin. *Photophores* on dorsal surface of head much reduced in size and number.

Three longitudinal rows of *photophores* on arms I, II, and III, dorsal and median row of small- and medium-sized organs respectively, ventral row of large organs. *Photophores* in terminal third of ventral row extraordinarily enlarged and heavily pigmented (Fig. 22, h). Most basal of these unique *photophores* largest, approximately three or more times size of normal organ; succeeding organs decreasing in size toward tip of arm; number varying with size of animal.

Arm IV with four conspicuous longitudinal rows of *photophores*, three rows of large organs and one row of intermixed medium and small organs along dorsal margin of arm; only median row of large organs extending to tip of arm. Two additional rows of minute *photophores* present in largest specimen. *Photophores* on IV all normal, none showing unusual enlargement found terminally on other arms.

Male genitalia single, on left side. Mature *spermatophores* present only in male of 51.0 mm ML (DANA Sta. 3975 VI), SpL 2.2 mm. Sperm mass very small, SpMI 2.79-3.59. Cement body long and slender, CBI 67.7-73.0; appears to lack oral connective complex with ejaculatory apparatus, giving rise to ejaculatory tube by simple tapering with initial one or two coils. Oral half of ejaculatory apparatus with one large loop.

Gladius (51.0-mm-ML specimen) delicate, typically deeply concave on ventral surface. Vane long, GLVI 76.3; width approximately 17 per cent of *gladius* length. Posterolateral margins of vane only slightly thickened and pigmented.

Lower *beak* with typical strong median ridge on lateral wall.

Radula of a specimen from Cook Strait illustrated. Approaches general

homodont condition with rhachidian and first and second laterals remarkably similar in size, shape, and base configuration; third laterals, only, being much longer. No marginal plates present.

Type.—British Museum (Natural History), BM 1890.1.24.18.

Type-Locality.—Mid-South Atlantic, 35°36'S, 21°12'W, 3700 meters.

Discussion.—The name *Histiopsis atlantica* first appeared in print in 1885 in Hoyle's narrative of the voyage of the H.M.S. CHALLENGER. Since neither a description nor an illustration were included, the name was a *nomen nudum*. Later that same year, however, Hoyle published a good detailed description of his new species, represented by a single specimen of 35 mm ML trawled by the CHALLENGER in the mid-South Atlantic. He erected the new genus, *Histiopsis*, because he considered his specimen to possess characters that placed it intermediate between the genera *Calliteuthis* and *Histioteuthis*. In 1886, in his "Report on the Cephalopoda Collected by the H.M.S. Challenger . . .," Hoyle gave additional data and quite adequate illustrations. In 1900, however, George Pfeffer synonymized the species as a juvenile of *Histioteuthis bonnellii* and elaborated on this move in his large monograph of 1912. Since that date, *atlantica* has been virtually ignored. An 8-mm juvenile illustrated by Lo Bianco (1903) and identified as *Histiopsis atlantica* Hoyle does not appear to belong to this species, or even to the family.

An examination of the type in the British Museum revealed it to be indeed as Hoyle had described and illustrated it. Though the clubs were lacking, as originally described, it still possessed the series of enlarged photophores on the ends of arms I, II, and III which so strikingly distinguish this species from all others in the family. Most of the photophore pattern was intact, as well as the sculpture of the dorsal pad of the funnel organ. The ventral arms were found to have four longitudinal rows of photophores and the dorsal three pairs of arms to have three rows, rather than the three and two rows, respectively, that were originally described by Hoyle.

Dell's description and illustrations of his species *H. cookiana* suggested a striking resemblance to *atlantica*. Upon request, Dr. Dell kindly loaned me the holotype, one of the paratypes, an additional specimen from the Cook Straits (the BANZARE specimen identified [Dell, 1959] as *Calliteuthis miranda* Berry), and two specimens collected by the TUI Oceanographic Cruise of Auckland University. With the exception of the one paratype of *cookiana*, all were found to be identical with *atlantica*.

Dell separated his original material of *cookiana* into two series, the "short webbed" and the "long webbed." The "short webbed" series, represented to me by the holotype, is the same as *atlantica*, while the "long webbed" series, represented by the paratype on loan to me, belongs to a

new species described elsewhere in the present paper. This naturally is dependent on the condition that the remaining paratypes that belong to the respective "series," but which are not available to me, are identical to those examined.

The acquisition of the additional specimens collected by the ELTANIN, GALATHEA, and DANA served to further clarify this species.

In *atlantica*, the unique series of enlarged terminal photophores on the dorsal three pairs of arms varies in number with the growth of the animal. In specimens of 24-34 mm ML, there are three to five organs developed in the series, while in the 53- and 91-mm-ML specimens, five to eight organs are developed. The smallest juvenile to have the arm tips intact was 12.8 mm; two terminal photophores were present on arms I, II, and III. In all specimens except the 12.8-mm one, the series on arms I, II, and III are comprised of a respectively decreasing number of organs.

The clubs of *atlantica*, missing in the type-specimen, are as unusual as the terminal series of photophores on the ends of the arms. The fewer, irregular appearing, rows of suckers on the manus and the extreme enlargement of the suckers of the central series are distinctive. The enlarged carpal sucker at the base of the manus displays an interesting variation. In four of the specimens, one from off Cape Town, South Africa, one from the southern Indian Ocean, and two from off the southern coast of Chile, this enlarged, smooth, ringed carpal sucker has a conspicuous crescent-shaped projection on the distal outside margin of the ring, extending from near the base of the sucker to the surface of the ring or above it (Fig. 32, g). None of the other specimens with clubs intact showed this apparent aberrancy.

Juveniles of *atlantica*, which may have the skin with the characteristic terminal photophores on the tips of the arms rubbed off, bear considerable resemblance to young *reversa*, but young *atlantica* as small as 7 mm ML are readily distinguishable by the medium depth of the inner web.

The available spermatophores that are described and illustrated were in such poor condition that it is possible that some structural details are lacking.

Remarks.—An interesting color note on the back of the label enclosed with the BANZARE specimen reads as follows: "General colour rich port wine brown with metallic lustre. In each pore bright spots of gold and cerise. Spots of luminous violet near tips of arms."

Distribution.—All of the specimens of *atlantica* were taken in a belt between about 35° and 52° S in the southern Atlantic, Pacific, and Indian oceans. Undoubtedly, the continuing work in the subantarctic region will greatly expand our present knowledge of this long-ignored species.

The majority of the specimens were taken in waters related to land

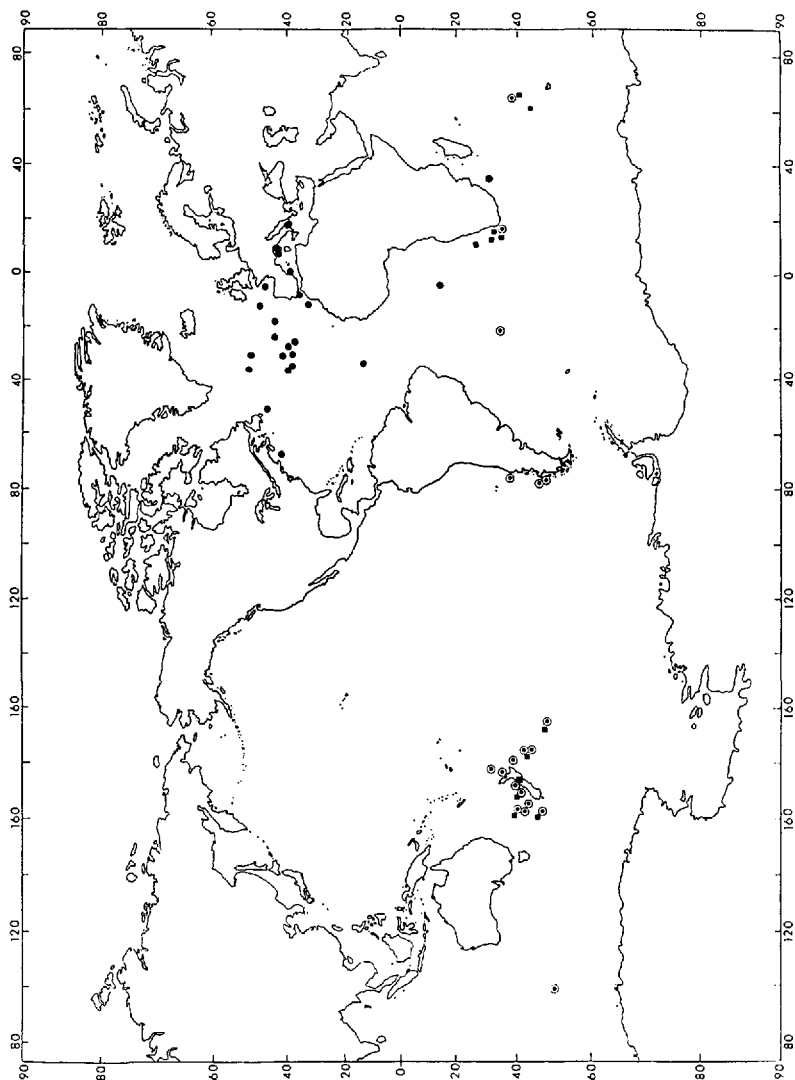


FIGURE 33. Distribution of confirmed, identified specimens. ● = *Histioteuthis bonnellii* (Férussac); ○ = *H. atlantica* (Hoyle); ■ = *H. macrohista*, n.sp.

masses. Analysis of the data shows that *atlantica*, collected in nets fishing at maximum depths of from 52 to about 3700 meters, occurs in greatest abundance between about 300 to 3000 meters with indications of a vertical migration.

Histioteuthis bonnellii (Férussac, 1835)

Figs. 6, g; 8, f; 33-35

Cranchia Bonnellii Férussac, 1835: pl. 66.

Histioteuthis Bonelliana (Férussac), d'Orbigny, 1848: 327, *Cranchia* pl. 2.—Gray, 1849: 45.—Verany, 1851: 114, pl. 19.—d'Orbigny, 1855: 380, pl. 25.—Tryon, 1879: 166, pl. 71, figs. 274-281.—Hoyle, 1886: 43.—Carus, 1889: 451.—Pfeffer, 1900: 170; 1912: 297, pls. 23-25.—Naef, 1916: 15, 18; 1921: 538.—Grimpe & Hoffmann, 1921: 179, figs. 1-8.—Degner, 1922: 215.—Naef, 1923: 362.—Grimpe, 1924: 328.—Joubin, 1924: 73.—Degner, 1925: 16, text-figs. 9, 10.—Bouxin & Legendre, 1936: 57.—Hardy, 1956: 289, fig. 96a.—Clarke, R., 1956: 257, figs. 3, 6.—? Rees & Maul, 1956: 267.—Arbocco, 1958: 117, fig. 1.—Morales, 1962: 106.—Clarke, M. R., 1962a: 3, fig. 3; 1962b: 439, pl. 15, figs. A-C.—Torchio, 1965: 266, figs. 2-3.

Cranchia Bonelliana Férussac, Verany, 1840: fig. 20.

Histioteuthis Ruppelli Verany, 1846: 28, pl. 3.—Gray, 1849: 45.—Verany, 1851: 117, pls. 20, 21.—Tryon, 1879: 166, pl. 71, fig. 282, pl. 72, figs. 283, 284.—Hoyle, 1886: 44.—Carus, 1889: 451.—Weiss, 1889: 83, pl. 10, figs. 8-12.—Jatta, 1896: 115.—Joubin, 1899: 73; 1900: 98, (in part: only specimens B, C, D).—Lozano y Rey, 1905: 182, fig. 59.—? Fischer & Joubin, 1906: 341.—Chun, 1906: 743; 1910: 147-169, 176, text-pl. 1, figs. 3, 4, pl. 21.

Histioteuthis Bonellii (Férussac), Verany, 1846: 29.—? Dell, 1959: 101.—Clarke, M. R., 1966: 194, figs. 38, 39.

Histioteuthis Collinsii Verrill, 1879: 241.—Tryon, 1879: 166.—Verrill, 1880c: 290, pl. 14; 1880d: 234, pl. 22; 1881a: 300, 404, pl. 27, figs. 3-5, pl. 37, fig. 5; 1882a: 331, pls. 23, 24; 1882b: 121, pls. 23, 24, figs. 3-6.—Hoyle, 1886: 44.

Histioteuthis bonnellii (Férussac), N. Voss in G. Voss, 1967: 74.

Material Examined.—HOLOTYPE OF *Histioteuthis Ruppelli* VERANY, 1846: 1 spec., ML 140 mm, off Nice, MHNN.

OTHER MATERIAL: 3 sex ?, ML 145-110 mm, PRINCESSE-ALICE Sta. 588, 38°34'45"N, 29°37'W, 18 July 1895, regurgitated by sperm whale, IOM (*H. Ruppelli*, Joubin, 1900: 98).—1 spec., ML approx. 120 mm, U.S. Bur. Fish. Acc. 153537, coll. Dr. Kendall, USNM.—1 ♂, ML 21.0 mm, DANA Sta. 4197 VII, 43°39'N, 24°04'W, 25 June 1931, mw 600.—1 ♀, ML 17.3 mm, IKMT No. 31, 32°30'S, 35°08'E, 12 Aug. 1962, 500 meters, SAM A29724.—1 ♂, ML 15.6 mm, DANA Sta. 3996 VII, 15°41'S, 5°50'W, 25 Feb. 1930, mw 600.—1 ♀, 1 ♂, ML 15.5-11.1 mm, DANA Sta. 4172 III, 43°05'N, 18°05'W, 1 June 1931, mw 400.—1 ♀, 1 ♂, ML 15.0-10.0 mm, DANA Sta. 1113 I, 36°10'N, 6°42'W, 17 Sept. 1921, mw 400.—1 ♂, ML 13.5 mm, ATLANTIS Sta. 143, 50°00'N, 35°20'W, 2 Sept.

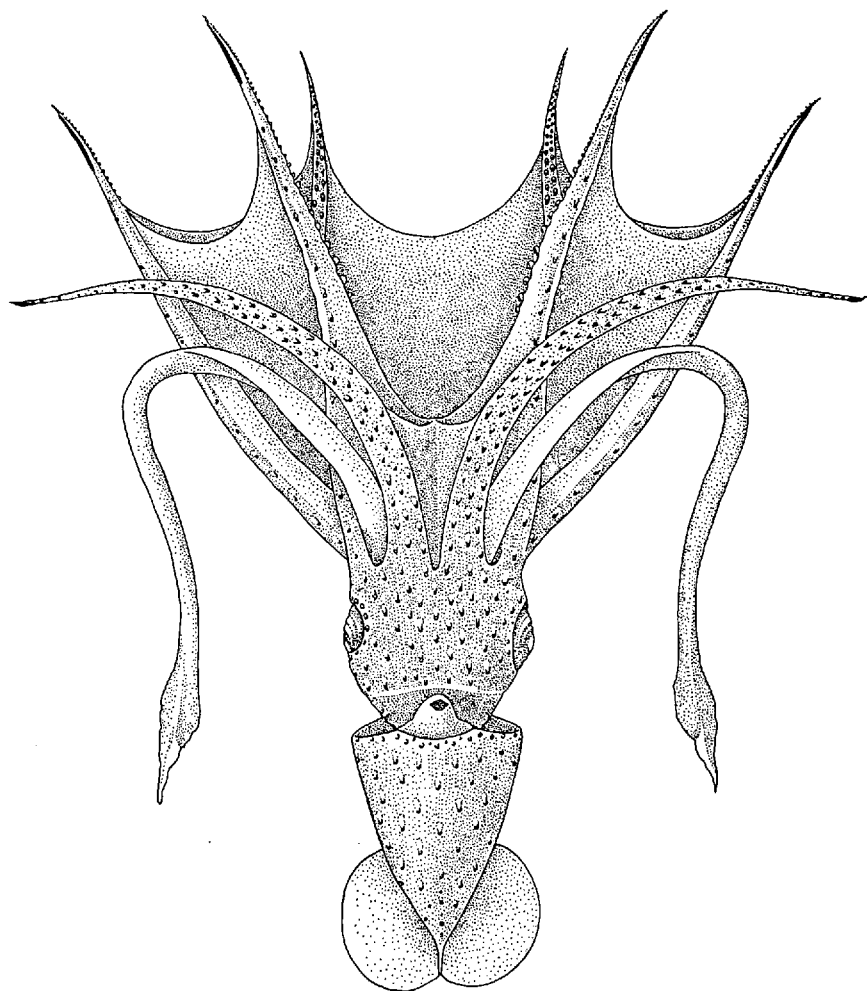


FIGURE 34. *Histiototeuthis bonnellii* (Férussac, 1835), ML 185 mm (redrawn from Pfeffer, 1912).

1928, 915 meters, MCZ 224810.—1 ♀, ML 13.4 mm, DANA Sta. 1163 IV, 12°59'N, 32°49'W, 11 July 1921, mw 300.—1 ♀, ML 12.2 mm, DANA Sta. 4158 XVI, 46°28'N, 8°01'W, 18 June 1930, mw 2000.—1 ♂, ML 12.0 mm, DANA Sta. 1374 VIII, 37°40'N, 26°00'W, 15 June 1922, mw 1000.—1 ♀, ML 11.2 mm, DANA Sta. 1377 IV, 37°40'N, 26°00'W, 15 June 1922, mw 300.—1 ♀, ML 10.7 mm, DANA Sta. 4158 XVII, 46°28'N, 8°01'W, 18 June 1930, mw 1500.—1 ♂, 1 sex ?, ML

10.6-9.0 mm, DANA Sta. 4169 III, 47°53'N, 14°29'W, 28 May 1931, mw 300.—1 ♀, ML 10.5 mm, DANA Sta. 1108 I, 35°11'N, 8°28'W, 14 Sept. 1921, mw 300.—1 ♀, ML 10.0 mm, DANA Sta. 4194 III, 41°56'N, 30°08'W, 21 June 1931, mw 300.—1 ♂, ML 9.7 mm, DANA Sta. 4172 IV, 43°05'N, 18°05'W, 1 June 1931, mw 300.—1 ♀, 1 ♂, ML 9.6-7.1 mm, DANA Sta. 4203 III, 49°49'N, 30°22'W, 30 June 1931, mw 300.—1 ♀, ML 8.8 mm, DANA Sta. 4018 II, 31°30'N, 12°12'W, 29 March 1930, mw 600.—1 ♀, ML 8.7 mm, DANA Sta. 1386 V, 45°15'N, 8°43'W, 24 June 1922, mw 200.—1 ♂, ML 8.7 mm, DANA Sta. 4190 VII, 37°58'N, 27°39'W, 14 June 1931, mw 400.—1 sex ?, ML 7.6 mm, DANA Sta. 4194 I, 41°56'N, 30°08'W, 21 June 1931, mw 500.—1 spec., PRINCESSE-ALICE Sta. 3279, 38°55'N, 34°07'30"W, 23 Aug. 1912, 0-3000 meters, IOM (*H. bonelliana*, Joubin, 1924: 73).—2 spec., PRINCESSE-ALICE Sta. 3281, 39°25'40"N, 35°14'30"W, 24 Aug. 1912, 0-4000 meters, IOM (*H. bonelliana*, Joubin, 1924: 73).—1 spec., PRINCESSE-ALICE Sta. 3284, 39°19'N, 35°24'30"W, 24 Aug. 1912, 0-1000 meters, IOM (*H. bonelliana*, Joubin, 1924: 73).—2 spec., PRINCESSE-ALICE Sta. 3285, 39°23'N, 35°18'30"W, 24 Aug. 1912, 0-500 meters, IOM (*H. bonelliana*, Joubin, 1924: 73).—1 large head, schooner AUGUSTA JOHNSON, lot 962, west end of Grand Banks, from stomach of cod, coll. Capt. Johnson, USNM 575322 (*H. Collinsii*, Verrill, 1881a: 404).—1 large head, schooner ALICE G. WONSON, lot 980, NE part of Georges Bank, coll. Capt. Anderson, 330 meters, USNM (*H. Collinsii*, Verrill, 1881a: 404).

Description.—Conical *mantle* relatively short, broad, width over one-half to approximately three-quarters of mantle length. Anteroventral margin slightly excavated beneath funnel with lateral angles blunt; median antero-dorsal margin produced into low, broad, obtuse angle.

Fins transversely oval in outline; large, length approximately one-half to two-thirds mantle length; width approximately three-quarters to equal of mantle length. Anterior margins free; posterior margins extending for short distance beyond tip of mantle; lobes united posteriorly with median notch.

Funnel supported by double bridle. *Locking apparatus* typically histioteuthid with crescent-shaped ridge on mantle wall; matching groove in oblong cartilage on funnel. Dorsal member of *funnel organ* inverted V-shaped pad with moderately long slender arms and anterior apical papilla, permanent sculpture not apparent; ventral members two elongate kidney-shaped pads. Semicircular *valve* present.

Asymmetrical *head* large, exceeding mantle in width; eyes display typical strong asymmetry. *Olfactory organ* ventral to single *nuchal fold*.

Buccal membrane with six lappets and six supports. Middorsal or first support bifurcate through web to dorsal sides of arms I; second supports to dorsal sides of II; third supports to ventral sides of III; fourth support

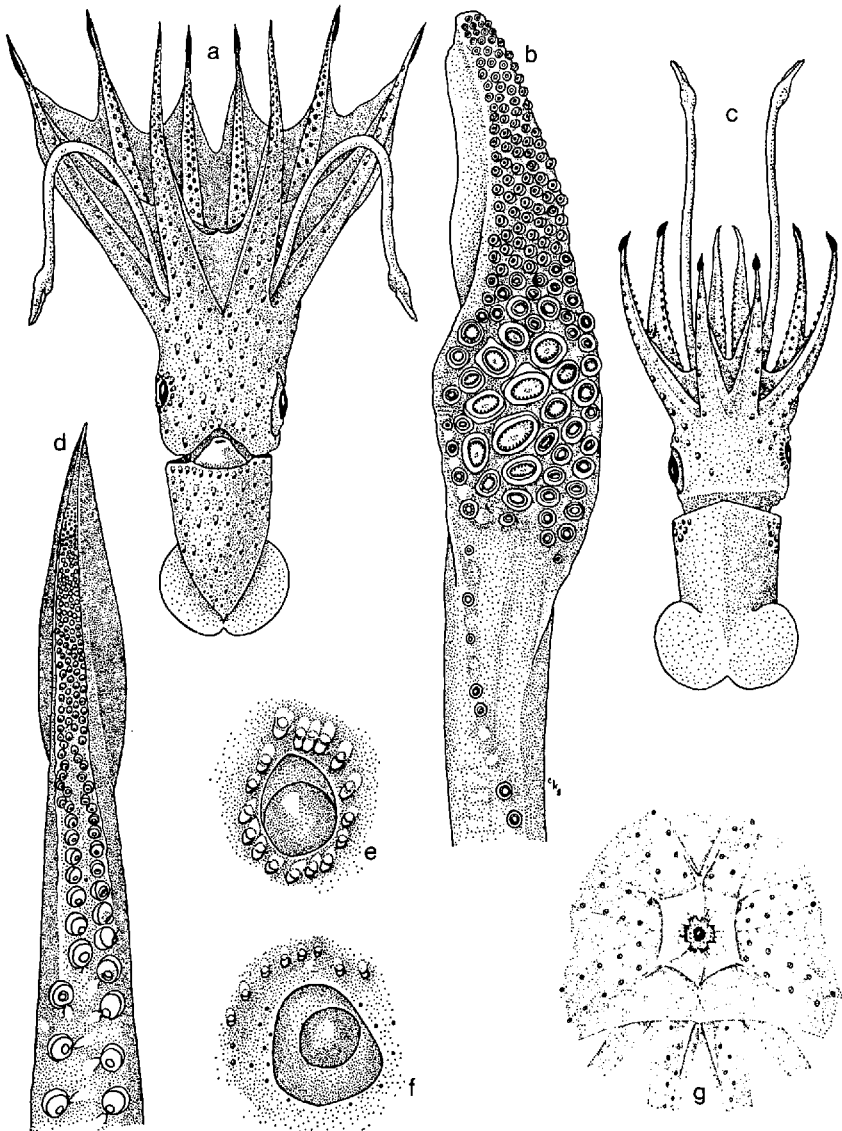


FIGURE 35. *Histioteuthis bonnellii* (Férussac, 1835): a, ventral view, *D* 4197 VII, male, ML 21.0 mm; b, left tentacular club of same; c, dorsal view, *D* 4190 VII, ML 8.7 mm; d, distal end, right arm I, *D* 4197 VII, male; e, right eyelid of same; f, left eyelid of same; g, buccal view of same.

with multiple attachments, one strand each to dorsal sides of arms IV and double strand to midline junction of web segments from arms III with those from arms IV (Fig. 35, g). *Inner web* connecting arms I, II, and III deep, approximately 50 to over 60 per cent length of longest arm (measurement taken at midpoint of web); deepest segment between arms II and III. In large specimens, origin of web from arm approximately coincides with base of enlarged terminal photophore. *Outer web* slightly developed in large specimens.

Arms strong, stout at base, tapering distally to delicate tips; long, two to over three times mantle length. Arms III and II longest, about coequal; arms I and IV about coequal; approximate arm formula, $3 = 2.1 = 4$.

Aborally, *swimming keel* originates in basal half of IV, expanded for distance less than one-quarter length of arm, then reduced to low keel to tip of arm. Low median *keel* on distal half to two-thirds of arms I and II; keels extend over enlarged terminal photophore.

Biserial *suckers* arranged along outer margins of oral surface of arms; roughly uniform in size until they regularly decrease as arm tapers to tip. Suckers of IV about two-thirds size of those of other arms. *Horny rings* usually armed with four to five broad, blunt teeth on distal margin.

Distal ends of both dorsal arms of male *hectocotylized*.

Protective membranes developed into deep inner web described earlier.

Tentacles long, approximately two to three times length of mantle, terminating in expanded club in which broad manus and attenuate dactylus are of about equal length. *Carpal adhesive apparatus* on oral surface of tentacular stalk extends about two club-lengths proximal to manus. Commencing at this distal point, elements arranged in uniserial order along ventral margin as follows: 1 s, 2 pp, 2 ss, 2 pp; then diagonally across stalk 2 ss, 2 pp; continuing up dorsal margin 2 ss, 1 p, 1 s, 1 p, 1 s, 1 p, 1 s; extending up dorsal margin of manus, arrangement continues as 1 p, 1 s, 1 p, 1 s, 1 p, 1 s, 1 p, 1 s.

Suckers of manus set in about five rows, those in second and third rows from dorsal margin enlarged. Entire margins of *horny rings* armed with fine sharp teeth. Suckers on dactylus, uniformly decrease in size; at first set in rows of six, then fewer as dactylus tapers. Low *protective membrane* on either margin of manus, reduced on dactylus.

Median *swimming keel* on distal half of aboral surface of club; no longitudinal *cleft* on proximal half. Strong, low, median keel often present on stalk proximal to club.

Photophores on ventral surface of mantle regularly set in about seven diagonal rows; uniformly large on upper half with exception of irregular scattered minute organs; photophores on posterior half of mantle, regularly reduced in size. Photophores on dorsal surface of mantle much reduced in size and number, appearing less regularly arranged in diagonal rows.

TABLE 14
MANTLE MEASUREMENTS (IN MM) AND INDICES OF
Histioteuthis bonnellii (FÉRUSSAC, 1835)

	*	**	***	****	D 4197 VII	SAM A29724	D 3996 VII	D 4172 III	D 1113 I	D 1163 IV	D 4158 XVI
	♂	—	—	—	♂	♀	♂	♂	♂	♀	♀
ML	165	145	140	69	21.0	17.3	15.6	15.5	15.0	13.4	12.2
MLI	—	—	18	24	27.7	25.2	28.4	25.7	30.5	32.7	29.0
MWI	—	—	86	62	61.8	62.3	64.0	67.0	62.0	—	59.0
HLI	55	52	67	65	72.8	72.2	76.2	72.8	73.3	—	57.4
HWI	61	—	83	62	90.5	109.8	89.5	87.2	93.3	89.5	86.0
FLI	53	59	53	70	61.8	58.9	58.4	62.0	66.6	53.0	61.5
FWI	76	90	87	99	80.7	98.3	82.0	92.3	94.5	82.0	91.0
AI I	200	238	286	239	152.4	144.5	141.0	159.4	120.0	105.2	123.0
II	194	279	386	239	164.3	166.0	160.3	174.8	145.4	112.0	139.3
III	197	310	372	239	171.4	189.0	147.5	187.0	146.8	113.5	146.6
IV	164	238	307	239	119.0	150.4	109.0	154.2	108.8	97.0	94.2
TLI	206	—	576	392	228.5	324.0	197.5	348.5	104.8	269.3	142.0
CLI	—	—	—	—	32.8	30.6	32.7	38.7	33.3	31.3	30.3
M+I	—	—	—	—	18.1	19.1	14.1	21.3	22.0	22.4	25.4
IWI A	—	—	—	58	50.5	41.0	49.5	46.5	41.4	46.0	26.7
B	—	—	—	58	55.5	39.1	49.5	35.5	49.0	57.5	—
C	—	—	—	58	61.0	39.7	56.7	46.2	50.4	52.6	34.5
D	—	—	—	—	31.9	—	32.0	—	22.7	34.2	—
E	—	—	—	—	33.3	28.5	26.0	—	30.9	33.6	—

* Chun (1909: 176), from original measurements.

** Jatta (1896: 117), from original measurements.

*** Verany (1851: 117), type of *H. Ruppellii*, from original measurements.

**** Verany (1851: 114), from original measurements.

Photophores on ventral surface of head set in diagonal rows, with exception of cirlet of organs around eyelids. Seventeen large photophores closely set around margin of right eyelid, in addition to arc of seven large photophores over anterior and ventral margins of left eyelid, a cirlet of about 11 small photophores present around more immediate ventral, posterior, and dorsal margins. Photophores on dorsal surface of head much reduced in size and number.

Three longitudinal rows of photophores on bases of all four pairs of arms. On arms I, II, and III, photophores in dorsal row minute, those in median row of medium size, those in ventral row of large size; only ventral row of large photophores approaches distal end of arms where single, greatly enlarged photophore occupies entire tip. Large terminal photophore 12-15 per cent length of respective arm, follows taper of arm tip but exceeds its outline.

Dorsal row of 13-14 photophores on arms IV extends two-thirds length of arm; ventral row terminates just short of tip, with only median row

TABLE 14 (Continued)
 MANTLE MEASUREMENTS (IN MM) AND INDICES OF
Histioteuthis bonnellii (FÉRUSSAC, 1835)

	D_{1374} VIII ♂	D_{4158} XVII ♀	D_{4169} III ♂	D_{1113} I ♀	D_{4194} III ♀	D_{4172} IV ♂	D_{4203} III ♂	D_{4169} — III	D_{4018} II ♀	D_{4190} VII ♂
ML	12.0	10.7	10.6	10.0	10.0	9.7	9.6	9.0	8.8	8.7
MLI	30.0	31.5	28.6	35.3	33.1	26.9	36.9	34.6	36.5	34.8
MWI	66.6	60.7	56.6	60.0	53.0	73.2	52.3	58.9	56.8	59.7
HLI	65.8	65.5	56.6	52.0	69.0	72.2	52.0	64.5	58.0	57.5
HWI	106.0	75.7	92.5	92.0	88.0	93.8	73.0	70.0	83.0	82.8
FLI	67.5	59.8	59.5	62.0	58.0	64.0	54.2	56.6	56.8	59.8
FWI	100.0	94.3	94.2	92.0	88.0	104.0	83.3	88.8	83.0	84.0
AI I	134.0	131.0	131.0	100.0	110.0	139.2	91.5	103.3	102.5	92.0
II	158.2	144.0	139.6	116.0	132.0	165.0	102.0	111.0	114.8	104.7
III	158.2	150.5	149.0	127.0	116.0	186.9	113.6	122.2	125.0	115.0
IV	104.0	131.0	129.2	110.0	102.0	135.0	85.4	91.2	90.0	92.0
TLI	—	148.6	256.5	125.0	190.0	351.0	187.5	227.8	205.0	205.0
CLI	—	36.1	37.7	30.0	30.0	43.3	32.3	41.1	31.8	35.6
M+I	20.8	26.2	28.3	20.0	20.0	20.6	20.8	21.1	22.7	23.0
IWI A	26.3	24.8	19.0	23.6	22.7	21.0	17.4	18.2	19.1	27.0
B	34.7	26.7	25.3	23.6	30.3	26.0	18.4	20.9	23.6	29.0
C	31.6	31.0	30.4	28.3	37.2	32.6	25.7	27.2	28.2	30.0
D	33.7	23.6	19.0	15.7	22.7	22.1	18.4	18.2	24.6	20.0
E	23.7	12.4	19.0	11.0	21.2	17.7	18.4	14.6	18.2	20.0

extending to end of arm. Normal large photophores in all three rows, no enlarged terminal photophore present.

Male genitalia single, on left side.

Gladius, beaks, and radula not dissected out because of small size of material available. The beaks and radula (Figs. 6, g; 8, f) were redrawn from Naef (1921). Median ridge present on lateral wall of lower *beak*. *Radula* definitely heterodont; first and second laterals asymmetrical with rudimentary cusp on outer end of rather long narrow base. Third laterals normal, long, saber-shaped. Weak marginal plates present.

Type.—Whereabouts unknown.

Type-Locality.—Mediterranean, off Nice.

Discussion.—This species was first inadequately described by Férussac in 1835 from a 70-mm-ML specimen taken alive in the Mediterranean by Verany. Férussac named it *Cranchia Bonnellii*, "en mémoire de l'excellent et célèbre professeur de Turin." Though the original plate was not available, that published by Férussac & d'Orbigny (1834-1848), a color reproduction of the original, was available. It compensates for some of

the inadequacies of the description and, among other valuable characters, illustrates the six-membered buccal membrane.

Winckworth (1942), in tracing the history of the completed work, *Histoire Naturelle Générale et Particulière des Céphalopodes Acétabulifères* by Férussac & d'Orbigny (1834-1848), found that it is a composite of 21 parts and 144 plates that were published over a period of 14 years under separate authorships prior to being collected into the final completed work, which was published in 1848 under dual authorship. In this latter collected work, the plate of the species in question is labeled "*Cranchia Bonelliana*, Férussac," a change from the original label "*Cranchia Bonnellii*, Férussac," as published by Férussac in 1835. An "n" has been dropped in the specific name and the ending changed from "i" to "ana." These changes are attributed to d'Orbigny. In Férussac's day, it was common for a person's name to be spelled more than one way, and, since Férussac did not spell out the name of the professor from Turin in the original work, there is no "clear evidence of an inadvertent error"; I feel, therefore, that his original spelling, *Bonnellii*, is valid and must be retained.

D'Orbigny's description in the collected work (1848) bears the altered specific name and places the species into a new genus *Histioteuthis*, which he had created for the species in an earlier part (1839), prior to its collection into the final work. In his expanded description of the genus, the six-parted buccal membrane was described for the first time.

In 1846, in the *Guida di Genova* (I have been unsuccessful in locating this work), Verany described and figured a new species, *Histioteuthis Ruppelli*, which he distinguished from *bonnellii* primarily by the irregular length of the arms and the web segments, the shape of the mantle and certain features of color. He further elaborated on the description in 1851. At the Musée d'Histoire Naturelle in Nice, a large specimen with a present mantle length of 148 mm was located with the following label in what appeared to be Verany's handwriting: "*Histioteuthis Ruppellii* Verany, Nice, 1857 (coll. Verany 49) type de l'espece." An examination of this specimen and a study of all other specimens identified in the literature as *ruppelli* and accompanied by a description (most of which I have examined), show them all to be normal *bonnellii*. Thus nothing remains to separate this species.

In 1879, Verrill described a new species, *H. Collinsii*, based on a large head with arms and tentacles intact recovered from the stomach of an *Alepisaurus ferox* off Nova Scotia. He later identified several mandibles and incomplete specimens with this species. The type could not be located, but two of Verrill's later specimens (1881a: 404) were examined at the U. S. National Museum. No features in these specimens or in any of Verrill's descriptions or illustrations warrants recognition of his species.

In 1900, Pfeffer synonymized *ruppelli*, *collinsii* and *Histiopsis atlantica* Hoyle with *bonnellii*. By synonymizing *Histiopsis atlantica* as a juvenile of *bonnellii*, Pfeffer gave rise to the concept of a seven-membered buccal membrane in the young and six-membered buccal membrane in the adult of this species. This was variously discounted by Naef (1923), Grimpé (1921, 1924), Degner (1922, 1925), all of whom also discussed various other features of development of the species.

The type of *Histiopsis atlantica* has been examined at the British Museum and found to represent a very distinct separate species, as Hoyle originally described it. It, together with identical additional material, is discussed elsewhere in this paper under that name (p. 823).

Strangely enough, there does exist a species very closely related to *bonnellii* which shares all the more obvious characters such as the deep web, the single, large, elongate terminal photophore on arms I, II, and III, and the general photophore pattern, but has a seven-membered buccal membrane rather than a six-membered one. As far as I can determine, only one lot of specimens recorded in the history of *bonnellii* and its synonyms belongs to this latter species, which I describe as new elsewhere in this paper (p. 845). This lot consisting of two specimens taken off South Africa is recorded by Robson (1924a: 4; 1924b: 608).

Massy (1909: 29) identified as *H. bonelliana* four juveniles measuring 4-23 mm ML taken off the coast of Ireland. She described the three larger specimens (10-23 mm ML) as having no trace of web or enlarged terminal photophore on the arms. Since in this size range both these characters are very much in evidence in *bonnellii*, obviously, Massy's material is not of this species. Pfeffer (1912: 270) referred the larger specimen to *Calliteuthis Meneghinii* (= *H. reversa*). Massy (1913) concurred and also referred the second larger specimen from her earlier paper to that species. Actually, sufficient information for specific identification of any of her material is lacking.

The several undescribed large specimens merely listed by Joubin (1924) were examined in Monaco and are *bonnellii*.

H. bonnellii Férussac may be distinguished from all other histioteuthids by the following combination of characters: the exceedingly deep inner web connecting the arms, the single greatly enlarged elongate photophores borne terminally on arms I, II, and III, and the six-membered buccal membrane.

The juveniles of *bonnellii* can be easily distinguished down to a very small size. Even in specimens of 8-10 mm ML, the inner web may measure as much as 30 per cent of the longest arm. In the smallest specimen examined (7.1 mm ML) the large terminal photophore on the dorsal three pairs of arms was discernible. In juveniles of about 15-21 mm ML, this photophore already measures 12-15 per cent of the respective arm.

Growth is accompanied by an increased proportional length of the arms and an increased differentiation in the sizes of the suckers of the manus. Hectocotylization was evident in the smallest male available (8.7 mm ML). In the 21-mm-ML male, slightly less than the distal fifths of arms I were hectocotylized.

Chun (1910) stated that the hectocotylus of *H. Ruppellii* (= *bonnellii*) has four rows of suckers. His accompanying illustration is poor, the arms being obviously contracted and maimed in part. All of the large males of *bonnellii* available to me had the hectocotylus only partially intact, but the examination of what remained, together with those of the small males, leads me to question Chun's statement of four rows. The suckers are so closely set and the pedestals so enlarged that, if the arm is contracted, the suckers appear to fall into more than two rows. However, if a probe is laid down the median channel of the hectocotylus and then pressed outward against the suckers to one side, the suckers appear to fall into a single marginal row. This can easily be resolved in the future with the examination of large males in good condition.

Though the funnel organ in most of the specimens was unsculptured, a longitudinal ridge did appear on the arms of the dorsal pad in some specimens, but from the small size of the available material, it cannot be determined whether the ridge is an artifact of pressure or a permanent character.

The specimen from the Indian Ocean off South Africa was typical in comparison with the Atlantic and Mediterranean material, except for slight differences in the number of photophores around the margin of the left eyelid. Rather than having a ring of about 11 small photophores around the ventral, posterior, and dorsal margins of the eyelid, the Indian Ocean specimen had only one or two small photophores.

Unfortunately the greater amount of my study of this species was done on juvenile material, 21.0 mm ML and under. Good, complete, large adult specimens in the European museums were available very early in my study and only for the short period of examination that my necessarily brief visit permitted; they could not be referred back to for further study on certain details. My description and discussion may reflect this lack, and I hope that any resultant discrepancies are not too blatant.

I have found no reference to the depository of Férussac's type specimen, and though I could not locate it, my search was not exhaustive; thus I do not consider it permissible nor necessary at this time to select a neotype for this well-described species.

Remarks.—In the Discovery Report on the sperm whales of the Azores, R. Clarke (1956) found that squids were the staple diet, and that in 39

whales examined, 59 per cent of the squid present in the stomachs were *H. bonnellii*.

In a stomach analysis of a bull sperm whale caught off Madeira, M. R. Clarke (1962a) concluded that *bonnellii* was represented by 88.3 per cent of the 4000 beaks present in the stomach, and of the 28 partially intact squids present, 20 were of this species. Certainly, one may conclude that *bonnellii* is a prominent member of the pelagic community in these areas.

Verany (1851: 115) gave a glowing description of his 69-mm-ML animal while alive:

A general light rose hue fading to violet, covered by very bright carmine-red chromatophores, some larger, others very small, the coloring of a very brilliant red lacquer; the umbelliferous membrane is of a very beautiful velvety crimson; the arms on the internal face are of the same color, but their extremity is of an ultramarine blue. The ventral surface of the body is regularly lightly strewn with double united spots, disposed in quincunx, of which the lower are opaline-yellow, the upper smaller and blue of which it might be said that these latter are very brilliant sapphires and the former are topazes set into the skin. These same spots very regularly circle the eye opening, they are regularly distributed on the ventral and lateral parts of the head, and disappear on the dorsal part of the body and on the mediodorsal of the head; they are very regularly disposed in three rows on the arms of the first pairs, and in five on those of the fourth; those of the lateral rows are the larger and the more brilliant, and diminish very progressively towards the extremity of the arms. At the point of attachment, the fin is yellowish, the rest is livid rose-white; it is marked by very fine chromatophore points, carmine-red lacquer.

The eyeball is white, irised by blue; the eyelid maroon.

The tentacular arms pale rose, covered with red lacquer chromatophore spots; the club of a greenish yellow shade bordered by carmine red. The suckers of the sessile arms are each of a very brilliant ultramarine blue. The buccal membrane, white without chromatophore spots. (Translated from the French.)

This species attains considerable size; the largest recorded specimen had a mantle length of 330 mm, with a total length of 1190 mm (Morales, 1962).

Distribution.—From confirmed reports in the literature and from the specimens in this paper, *H. bonnellii* is known to be distributed throughout the North Atlantic south of approximately 50°N, in the Mediterranean Sea, and in the Indian Ocean off South Africa.

Individuals have been taken from the stomachs of sperm whales and various species of fishes and collected in the free state by nets fishing to maximum depths of approximately 70 to 2000 meters. Data analysis shows this species to be most abundant at depths between about 100 to 600 meters.

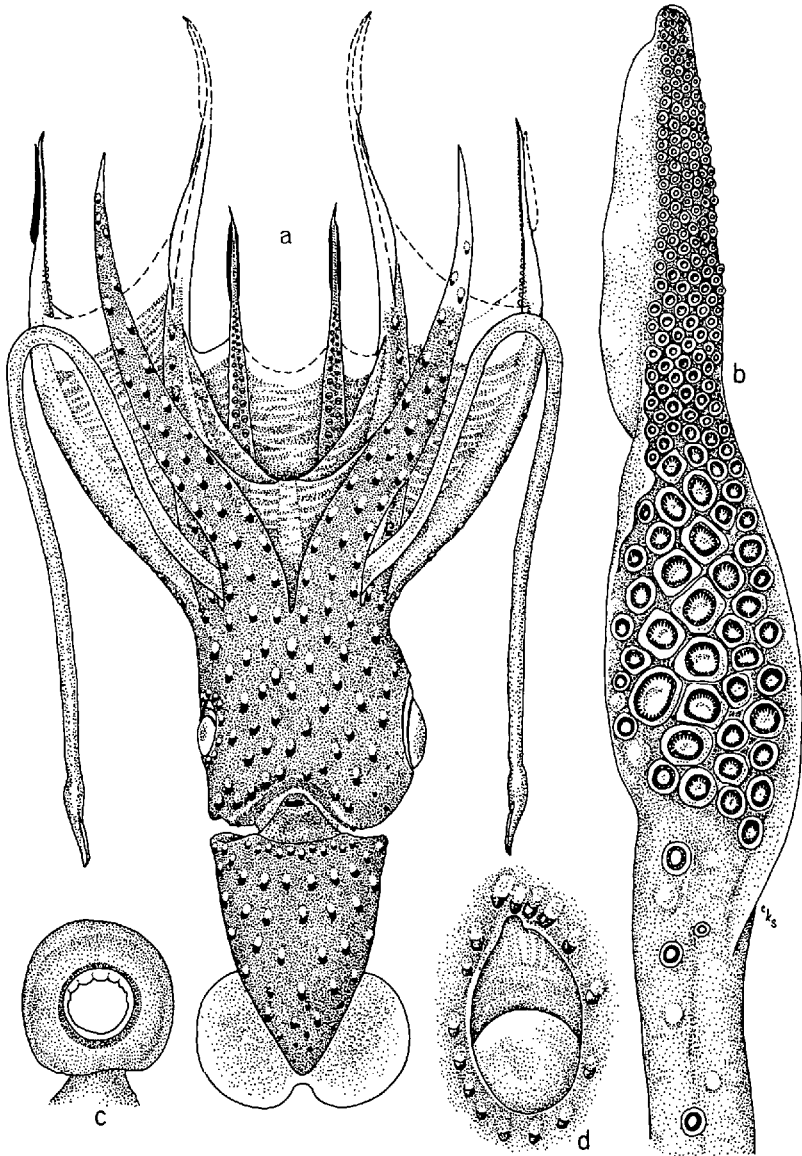


FIGURE 36. *Histioteuthis macrohista*, n. sp., holotype, USNM 576761, ML 52.0 mm: a, ventral view; b, left tentacular club; c, sucker from middle of right arm III; d, right eyelid.

***Histioteuthis macrohista*, n. sp.**

Figs. 4, a, b; 6, f; 8, g; 33; 36; 37

Histioteuthis Bonelliana (Férussac), Robson, 1924a: 4; 1924b: 608, figs. 9-12.*Histioteuthis cookiana* Dell, 1951: 1 (in part: two of the paratypes, designated as the "long webbed" series); 1952: 119 (in part: same as above).*Histioteuthis* sp. G. Voss, 1967: 75.

Material Examined.—HOLOTYPE: 1 ♀, ML 52.0 mm, ELTANIN Sta. 1834, 45°10'S, 160°10'E, 11 Dec. 1966, 700-780 meters, USNM 576761.

PARATYPES: 1 ♀, ML approx. 55 mm, IKMT No. 18, west of Slangkop, South Africa, 9 Sept. 1961, 400 meters, SAM A29637.—1 ♂, ML 40 mm, Cook Strait, New Zealand, from stomach of ling, *Genypterus blacodes* (Bloch & Schn.), DMNZ M17970.—1 ♀, ML 29.2 mm, ELTANIN Sta. 1704, 43°50'S, 174°27'W, 22 May 1966, 725-800 meters, 3-m IKMT, USNM 576176.—1 ♂, ML 25.1 mm, ELTANIN Sta. 1695, 47°18'S, 167°36'W, 18-19 May 1966, 368-658 meters, 3-m IKMT, UMML.—1 ♂, ML 23.6 mm, A. BRUUN Cr. 6, Sta. 354A-7340, 40°48'S, 65°03'E, 4 Aug. 1964, 0-1650 meters, 10-ft IKMT, USNM 576177.—1 ♀, ML 21.0 mm, A. BRUUN Cr. 3, Sta. 160-7132, 41°07'S, 59°52'E, 12 Sept. 1963, 150-635 meters, IKMT, UMML.—1 ♂, 1 ♀, ML 16.5-13.3 mm, DANA Sta. 3979 I, 27°10'S, 8°59'E, 15 Feb. 1930, mw 1000.—1 ♀, 1 ♂, ML 14.6-14.0 mm, DANA Sta. 3978 VI, 30°15'S, 13°15'E, 13 Feb. 1930, mw 5000.—1 ♀, ML 12.1 mm, DANA Sta. 3978 II, 30°15'S, 13°15'E, 13 Feb. 1930, mw 600.—1 ♀, ML 8.7 mm, DANA Sta. 3979 II, 27°10'S, 8°59'E, 15 Feb. 1930, mw 600.

OTHER MATERIAL: 1 ♀, ML approx. 67 mm, SS PICKLE Sta. 343, 30°10'S, 14°33'E, 5 May 1921, 860 meters, coll. J. D. F. Gilchrist.—1 ♂, ML 46 mm, SS PICKLE Sta. 542, 33°41'S, 17°09'E, 8 Dec. 1921, 1755 meters, coll. J. D. F. Gilchrist.—5 ♀♀, 3 sex ?, ML 12.7-6.0 mm, DANA Sta. 3978 IX, 30°15'S, 13°15'E, 13 Feb. 1930, mw 2000.—2 sex ?, ML 11.3-10.0 mm, ELTANIN Sta. 1825, 39°58'S, 160°34'E, 5 Dec. 1966, 1100-1625 meters, 3-m IKMT.—2 sex ?, ML 10.5-9.6 mm, ELTANIN Sta. 1817, 40°07'S, 168°05'E, 2 Dec. 1966, 375-405 meters, 3-m IKMT.—1 sex ?, ML 7.2 mm, ELTANIN Sta. 1834, 45°10'S, 160°10'E, 11 Dec. 1966, 700-780 meters, 3-m IKMT.

Description.—Mantle conical, short, width over one-half to almost three-quarters mantle length; posterior tip blunt. Anteroventral margin slightly excavated with blunt lateral angles; mid-anterodorsal margin produced into broad obtuse angle.

Transversely oval *fins* large, length approximately half that of mantle, width over three-quarters that of mantle. Posterior margins free, uniting short distance beyond tip of mantle, with median notch.

Funnel supported by typical double bridle. *Locking apparatus* crescent-

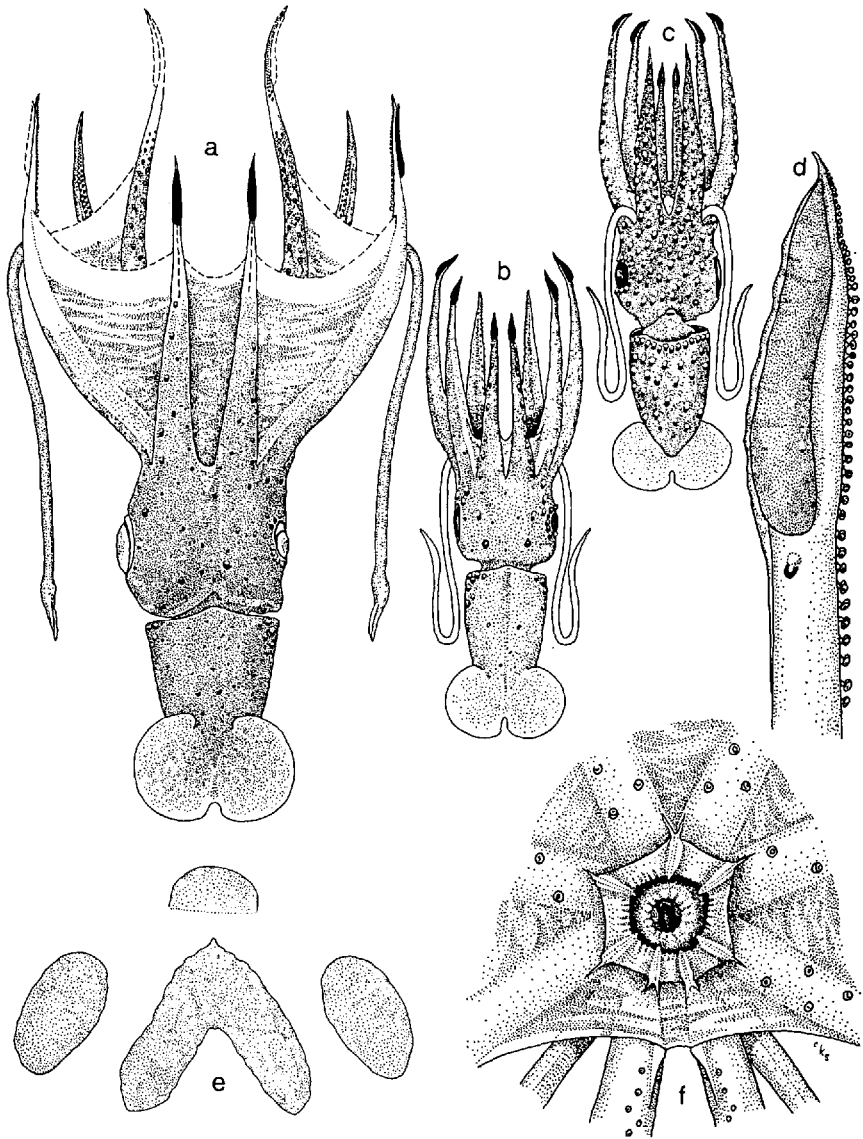


FIGURE 37. *Histiotteuthis macrohista*, n. sp.: a, dorsal view, holotype; b, dorsal view, *Elt* 1825, ML 11.3 mm; c, ventral view of same; d, lateral view of tip of right arm showing enlarged terminal photophore, paratype, DMNZ-M17970, ML 40 mm; e, funnel organ, paratype, SAM-A29637; f, buccal view, paratype, D 3978 VI, ML 14.0 mm.

shaped ridge on either side of inner wall of mantle; oval cartilage with deep, broad, longitudinal median groove on either side of outer wall of funnel. Dorsal pad of *funnel organ* inverted V-shaped with strong apical papilla; arms with swollen, heavy median ridge from anterior margin down entire length; oval ventral pads fleshy. Large semicircular *valve* present.

Very large asymmetrical head exceeds mantle in width. Left eye one-third to one-half larger than right. *Olfactory organ* papilla-like, ventral to single short *nuchal fold*.

Buccal membrane seven-membered with following attachments: mid-dorsal or first support bifurcate through web to dorsal sides of arms I; second supports to dorsal sides of II; third supports to ventral sides of III; fourth supports bifurcate, one strand to dorsal side of arms IV, one strand to web at point of juncture between web segment from III on its respective side and web between arms IV (Fig. 37, f).

Inner web well developed between all four pairs of arms in excess of 50 per cent of longest arm; segment between II and III deepest. Web segments from arms III fuse into web between arms IV at two separate junctures, one to either side of midpoint. *Outer web* slightly developed.

Arms long, length up to about twice mantle length; stout at base and tapering to slender tips. Arms III and II, and arms IV and I about coequal in length; approximate formula $3 = 2.4 = 1$.

Low *swimming keel* originates at about one-third arm length on aboral surface of III, elevated for less than one-half remaining distance of arm, thereafter continuing as low ridge to tip. Arms I and II with low keels distally; keel on all arms continuous over enlarged terminal photophores to be described later.

Small biserial *suckers* widely set, one row to either margin of arm; suckers largest on third quarter of arms. Suckers of IV approximately half size those on other arms. Distal margins of *horny rings* with about 4-10 low, square or rounded teeth, proximal margins irregular to smooth.

Hectocotylization of arms IV evidenced by long pedicels on suckers of distal third quarter of arms, thereafter suckers become very minute; suckers set in two rows throughout.

Protective membranes developed into deep inner web described earlier.

Tentacles slender, long, about two to four times mantle length, terminating in expanded club. *Carpal adhesive apparatus* extends about one and a half to two and a half club-lengths proximal to club on oral surface of stalk; from this point on left tentacle of holotype, uniserial arrangement begins on ventral margin with single sucker, followed by 2 pp, 2 ss then crossing diagonally 2 pp, 2 ss, to dorsal margin, thence 2 pp and 2 ss widely set in double row (ventralmost elements usually much reduced in size) followed by 1 p, and 1 s, thence on basal dorsal margin of manus 1 s, 1 p, 1 s, 1 p, and 1 s.

Suckers on *manus* arranged in about six rows; in large individuals, median few suckers of second and third rows medially from dorsal margin enlarged about twice size of other suckers. *Horny rings* armed with numerous sharp teeth around entire margin. Suckers on dactylus uniform, regularly reducing in size as club tapers; at first in rows of seven, reducing to four distally. Low *protective membrane* on either margin of manus and proximal dactylus.

On aboral surface of club, low *swimming keel* length of dactylus; no longitudinal *cleft* on manus.

Photophores on ventral surface of mantle uniformly large on anterior half, except for double anterior marginal row beneath funnel. Remainder large photophores in approximately six diagonal rows (approximately six to seven photophores in a row) relatively widely set. Photophores on posterior half of mantle regularly decrease in size; posterior tip free of large photophores. Few minute photophores scattered within overall pattern.

Dorsal surface of mantle with photophores reduced in size and number. Pattern often dominated by one or two pairs of large round photophores to either side of median line just anterior to anterior fin insertions.

Photophores on ventral surface of head spaced like those on ventral surface of mantle in diagonal rows, except for circlets around eyelids. Sixteen photophores form complete circlet around eyelid; circlet of about 8-11 very small photophores on immediate ventral, posterior, and dorsal margins of left eyelid, in addition to arc of large photophores over anterior and anteroventral margins. Two conspicuously large, round photophores widely set on left posterior margin of head, more median one the larger.

Photophores on dorsal surface of head reduced in number and in size except for two large organs, one to either side of median line at approximate level of posterior margin of right eyelid.

Three longitudinal rows of photophores on base of all four pairs of arms. On arms I, II, and III, photophores of dorsal row minute (not always apparent); those of median row medium in size; those of ventral row normal large size. Only latter row of large photophores extends to near distal end of arm, where entire tip is occupied by single, greatly enlarged, elongate photophore which tapers with arm but exceeds its outline.

All three longitudinal rows of photophores on IV composed of normal large organs; dorsal row of eight to nine photophores extends up two-thirds length of arm, ventral row terminates just short of distal end of arm, and only median row continues to tip, with decreasingly smaller photophores. No enlarged terminal photophores present.

Male with single set of *genitalia*, on left side. Mature *spermatophores* found in male paratype of 40 mm ML and in male of 46 mm ML (SS PICKLE Sta. 542). Sperm mass coiled, short, SpMI 7.14-8.32. Long,

slender cement body (CBI 67.0-73.7) terminates orally in constriction followed by connective complex of at least two distinct collars with intervening shallow cavities; ejaculatory tube rises from central pedestal, single long loop occupies two-thirds to three-quarters length of tube to cap.

Lateral wall of lower *beak* with moderately heavy median ridge.

Radula with first and second laterals only slightly asymmetrical; weak marginal plates present.

Type.—United States National Museum, USNM 576761.

Type-Locality.—Tasman Sea, 45°10'S, 160°10'E, 700-780 meters.

Discussion.—In 1924, Robson reported on two histioteuthids with mantle lengths of about 46 and 67 mm from South African waters; he referred these to *H. bonelliana*. He noted and described in some detail how his material differed from Pfeffer's and Chun's accounts of that species in the matter of the buccal membrane, the hectocotylus, and the club. Upon examination in the British Museum, I found that Robson's specimens were indeed different, and were identical to 15 juveniles collected by the DANA from South African waters and an additional large specimen from the same area sent for identification by the South African Museum. Thereafter, additional specimens were collected by the ships USNS ELTANIN and USRV ANTON BRUUN.

Dell's description (1951, 1952) of two of the paratypes of *H. cookiana*, which he referred to as the "long webbed" series, bore marked resemblance to this new material, and on request he kindly loaned me one of the specimens. It proved to be identical to the above material. From the collections of the South African Museum, the female of 55 mm ML that serves as a paratype for *macrohista* was referred to by G. Voss (1967) as *Histioteuthis* sp. In the literature on histioteuthids, I have found no other recorded specimen that is accompanied by adequate description, or that I have examined in the various collections, to be of this new species.

Superficially, *macrohista* could be mistaken for the closely related *bonnellii*, with its similar deep web; single, large, elongate terminal photophore on the first three pairs of arms; the general photophore pattern; and the overall proportions of the animal. A closer examination, however, reveals the striking differences, primary among these being the structure of the buccal membrane.

The buccal membrane in *macrohista* is seven-membered rather than six-membered as in *bonnellii*. The attachments of the first, second, and third supports are similar, but in *macrohista* there are two fourth supports rather than one; each has a bifurcate attachment, with one strand to the dorsal side of IV, and one strand to the web at the point where the web segment from III, on its respective side, joins the web between arms IV. The web segments from the two third arms do not join into the web between the

TABLE 15
MANTLE MEASUREMENTS (IN MM) AND INDICES OF *Histioteuthis macrohista*, n. sp.

	Holotype Elt 1834	DMNZ M17970	Paratypes									
			AB-3									
			Elt 1704	Elt 1695	160-7132	D 3979I	D 3978VI	D 3978VI	D 3979I	D 3978II	D 3979II	
	♀	♂	♀	♂	♀	♂	♀	♂	♀	♀	♀	
ML	52.0	40.0	29.2	25.1	21.0	16.5	14.6	14.2	13.3	12.1	8.7	
MLI	25.3	22.5	—	—	—	26.2	26.5	26.3	27.4	28.8	33.2	
MWI	67.3	71.3	58.5	59.7	73.3	70.2	69.0	70.4	68.5	67.0	60.9	
HLI	67.7	—	71.9	72.1	76.2	81.8	67.8	76.7	75.9	—	58.6	
HWI	94.2	—	—	91.6	106.9	79.4	89.0	—	88.7	82.5	80.5	
FLI	55.8	52.0	54.8	51.0	63.8	54.5	55.5	57.8	51.9	58.7	49.4	
FWI	88.5	79.5	84.5	80.0	91.5	84.8	90.4	90.1	91.0	85.0	81.5	
AI I	150.0	—	119.0	111.7	147.7	109.0	123.3	119.0	128.0	107.5	89.5	
II	184.7	—	152.0	—	179.4	157.0	164.5	137.2	167.0	140.5	160.8	
III	201.3	—	—	166.0	—	163.7	165.8	190.0	165.5	157.0	115.0	
IV	156.0	—	—	125.0	149.2	121.3	123.3	105.7	128.0	132.2	102.0	
TLI	346.0	386.0	—	263.0	306.0	317.0	413.0	310.0	332.0	273.0	164.3	
CLI	34.6	42.5	32.5	31.9	41.8	36.4	37.7	40.8	30.1	38.8	34.5	
M+I	13.5	17.5	—	14.7	—	24.2	27.4	23.2	22.6	24.8	23.0	
IWI A	—	—	—	—	32.9	35.9	—	—	36.0	—	19.2	
B	—	—	—	—	43.7	41.2	—	—	40.5	—	28.8	
C	—	61 (approx.)	—	41.7	50.5	40.7	—	—	45.0	—	28.8	
D	—	—	—	—	—	25.9	—	—	27.0	—	26.9	
E	—	—	—	26.2	27.8	25.9	—	—	22.5	—	19.2	

ventral arms at a near-common junction as in *bonnellii*, but rather at two widely separated points.

The funnel organ in *bonnellii* is apparently unsculptured, but in *macrohista* the dorsal pad bears a heavy swollen ridge down the length of each arm.

The carpal adhesive apparatus also differs noticeably between the two species, with *macrohista* having considerably fewer pads and suckers than *bonnellii*.

The general photophore pattern in both species is very similar. A consistent difference, however, is noted in the number of photophores forming the circlet around the margin of the right eyelid. Twenty-seven specimens of *bonnellii*, all with the pattern intact, had a count of 17 large photophores. Of 23 specimens of *macrohista*, 22 individuals had 16 and one individual had 15 large photophores in the circlet.

H. macrohista can be distinguished from all the remaining species of the family by the combination of characters of deep web; single, enlarged, elongate terminal photophore on the dorsal three pairs of arms; and the seven-parted buccal membrane.

Growth of the young is accompanied by a notably increased depth of the inner web and length of the sessile arms. The enlarged terminal photophore on the three pairs of dorsal arms could be easily distinguished even in the smallest 6.0-mm-ML specimen available. In specimens of 14.2-16.5 mm ML, its length was 17.0-18.7 per cent of the length of the respective arm. In the 52.0-mm-ML holotype, its length was 19.8-22.0 per cent of the respective arm. In all respects, this organ appears to be homologous to that in *bonnellii*.

In a few specimens, the swollen ridges on the dorsal pad of the funnel organ appeared to be deflated, thereby giving a folded appearance to the surface. In the female of 55 mm ML, the apical papilla of the dorsal pad was a bright pink color.

The inner web is far deeper than the measurements would indicate, because of the fact that the measurements were taken at the midpoint between two arms, which is really the lowest part of the segment. The actual emergence of the web from the arms in two large specimens of 40.0 and 55.0 mm ML coincided roughly with the base of the enlarged terminal photophore, thus giving a depth of approximately 83-86 per cent of the respective arm. (This also applies to the web of the previously described *bonnellii*.)

Unfortunately, the spermatophores of Dell's specimen from New Zealand waters were too deteriorated to show detail; the illustration and description given are those of the spermatophores from Robson's male collected by the SS PICKLE from South African waters.

Remarks.—The specific name *macrohista* is derived from the Greek *makros*, long, and *histos*, web, in reference to the long web, one of the most outstanding characters of this species.

Distribution.—All of the specimens of *macrohista*, a subantarctic species whose distributional range is just beginning to be known, have been taken between about 27° to 47°S in the South Pacific in waters east and west of New Zealand, in the South Atlantic from off the southwest coast of Africa, and from the southern Indian Ocean. Captured by nets fishing to maximum depths of approximately 200 to 2500 meters, *macrohista* appears to live chiefly between about 200 to 2000 meters.

Histioteuthis inermis (Taki, 1964)

Calliteuthis inermis Taki, 1964: 287, pl. 1, figs. 3-4, text-figs. 21-33.

This recently described species has not been included in the key or other taxonomic considerations in this paper because no material was available for study and, though Dr. Taki's description and illustrations are quite lengthy, certain essential details are lacking, possibly because of the condition of the three specimens. Opinions on the status of the species are given in the discussion following the description which is taken from that of Taki. The indices were derived from his published measurements.

Description.—Animal fleshy, rather firm; *mantle* short, conical in shape (MWI 58.7-68.6), widest just posterior to anterior mantle margin; sides gently convex; posterior tip rounded. Anteroventral margin broadly concave, anterodorsal margin produced forming obtuse angle.

Fins large, transversely oval in combined outline; length 45.7-54.8 per cent of mantle; width, 71.4-82.5 per cent of mantle. Posterior margin extends slightly beyond posterior tip of mantle; median margin with notch.

Funnel short, with two dorsal supports. *Funnel locking cartilage* elongate, ellipsoid in shape, slightly broader posteriorly than anteriorly. *Funnel organ* composed of broad, inverted V-shaped pad, with two broad, ellipsoid ventral pads. (From illustration, surface appears to be unsculptured, but perhaps swollen in appearance.) Semicircular *valve* present.

Head approximately as wide as mantle, eyes typically asymmetrical, with diameter of left eye being 1.55-1.7 times that of right. *Olfactory crest* thin, short.

Buccal membrane seven-membered. (From illustration, attachments of supports appear to be as follows: first support bifurcate to dorsal sides of arms I, second supports to dorsal sides of II, third supports to ventral sides of III, fourth supports to dorsal sides of IV). *Web* not described (from illustration, appears to be vestigial).

Arms rather stout, length one to one and one-half times mantle length;

TABLE 16
MANTLE MEASUREMENT (IN MM) AND INDICES* OF THE HOLOTYPE
AND TWO PARATYPES OF *Histioteuthis inermis* (TAKI, 1964)

	Holotype	Paratype No. 1	Paratype No. 2
ML	42	46	35
MWI	59.5	58.7	68.6
HLI	—	—	—
HWI	50.0	54.3	71.5
FLI	54.8	54.5	45.7
FWI	71.4	82.5	71.4
AI(L)I	135.7	111.0	108.6
II	152.2	119.5	120.0
III	136.0	117.2	125.6
IV	128.6	108.7	125.6
TLI	219.0	—	—

* Indices from measurements given by Taki (1964: 287).

arm order of two of three specimens, 2.3.1.4. *Swimming keel* originates at about two-fifths of an arm-length beyond proximal end of arm III.

Arm suckers of moderate size, largest suckers on arms I, II, and III, diameter 1.8 mm; those on IV, diameter 0.8 mm. *Horny rings* of suckers smooth on all arms.

Tentacles long, about twice as long as mantle, terminating in expanded club. *Club* with low *protective membrane* along both margins of oral surface. *Manus* with *suckers* arranged in five to six rows, of which, those of median two to three rows largest, approximately twice size of those of marginal rows; *horny rings* with 23 slender, pointed teeth equally spaced, those on proximal margin being thicker and lower than those on distal margin. Suckers on dactylus much reduced in size, in four to six rows, with *horny rings* entire. *Carpal arrangement* incomplete.

Photophores numerous on ventral surface of mantle. Large photophores uniformly set in about ten diagonal rows; photophores diminish in size near posterior end of mantle; approximately 14 medium-sized photophores in anterior marginal row. Photophores on dorsal surface of mantle smaller and fewer in number, set in about six diagonal rows.

Photophores on ventral surface of head both large and small, set in about six diagonal rows and posterior marginal row. Margin of right eyelid with circlet of 15-17 large photophores. Left eyelid with arc of five large organs over anterior margin and about six small ones on posterior margin. Dorsal surface of head with fewer and smaller photophores set in three diagonal rows.

Basal half of aboral surface of IV with three large longitudinal rows of large photophores; two rows extending onto distal half. Arms I, II, and

TABLE 17

COMPARISON OF *Histioteuthis inermis* (TAKI, 1964), *H. corona corona* (VOSS & VOSS, 1962), AND *H. corona berryi*, n. subsp.

	<i>inermis</i>			<i>corona corona</i>				<i>corona berryi</i>	
ML	46	42	35	54.5	42.0	38.0	32.0	47.4	36.0
MWI	58.7	59.5	68.6*	51.9	57.2	63.0	67.2	49.0	55.3
HWI	54.3	50.0	71.5	—	61.9	58.0	59.5	57+	63.9
FWI	82.5	71.4	71.4	64.2	60.3	73.7	68.8	61.2	65.0

* The high mantle indices (75.0-78.2) given by Taki (p. 29) for *inermis* are misleading because they were derived from the ventral mantle length, while those for *corona*, with which he compared them, were derived from the dorsal mantle length. All of the indices in the above table, as elsewhere in the present paper, were derived from the dorsal mantle length.

III with but one longitudinal row of photophores described, a ventral marginal row of large organs.

Knowledge of *genitalia* and *spermatophores* not available.

Gladius deeply pigmented; vane length 76 per cent of gladius length, width 28 per cent; rhachis deeply concave.

Radula with rather slender, long teeth, especially third lateral.

Type.—Zoological Institute, College of Science, Kyoto University, Japan.

Type-Locality.—Off Kambara, Suruga Bay, Japan.

Discussion.—Taki described his new species from the above holotype and two paratypes taken from Tosa Bay, Japan. Enquiry was made to Dr. Taki in regard to obtaining further information on the specimens and the possibility of borrowing material for study. Unfortunately, due to Dr. Taki's recent retirement and subsequent moving, the specimens and his notes were unavailable. Thus, in order to include *inermis* in the present work, it is necessary to rely solely on the original description and illustrations of this species.

Dr. Taki distinguished *inermis* from other known Pacific species, *japonica* (= *species dubia*, present paper), *dofleini*, *miranda*, *arcturi* (?= *dofleini*, present paper), and *celetaria pacifica*; and from the Atlantic species *corona*, of which he stated, "The present new species shows apparent resemblance . . . , though localities of both species are widely distant."

As itemized by Taki, the main differences between the two species *inermis* and *corona* are that *inermis* has a considerably broader mantle than *corona*; *inermis* has wider fins than *corona*; *inermis* has entirely smooth rings on the suckers of the distal parts of the arms, but *corona* usually has toothed rings; and *inermis* has 23 teeth on the manus suckers of the tentacular club, but *corona* has 33-35 teeth.

These differences are considerably minimized after the study of the additional material of *corona* that has been acquired since the original

description in 1962, the latter being the only information available to Dr. Taki. As discussed in the present paper, the known range of *corona* has been extended into the Indian Ocean and the northeastern Pacific, a fact which increases the probability of its occurrence in Japanese waters. The specimens from the northeastern Pacific, which for reasons discussed earlier, represent a distinct subspecies named *corona berryi*, show the same variation as *inermis* in regard to a reduced number of teeth on the rings of the manus suckers. In *c. berryi*, there are 28-30 teeth, against the 33-55 common in *c. corona*; Taki gives 23 as the count in *inermis*.

A comparison of the indices for the widths of the mantle, head, and fins of the three forms, in comparable size ranges, can be seen in Table 17. It can be seen that no distinct differences exist among the three forms.

The complete smoothness of all of the rings of the arm suckers as reported by Taki for *inermis* may be a good distinctive character, but study of the histioteuthids has shown the exact dentition, or lack of it, to be unreliable as a sole character for specific distinction. The radulas of *inermis* and *c. corona* compare very well. Even though little remains of the described differences between *inermis* and *corona*, one hesitates to synonymize *inermis* or perhaps name it as a subspecies of *corona*, which it might well be. It is thought best to withhold judgment for, in view of our added knowledge of *c. corona* and *c. berryi*, further study of Taki's specimens and possibly additional material is necessary in order to determine the true status of this species.

INDETERMINATE SPECIES

Several doubtful species and misidentified specimens that have appeared in the literature of the Histioteuthidae but have not been discussed or do not belong to the synonymies of the preceding described species are treated in the sections that follow.

SPECIES DUBIA

Loligopsis ocellata Owen, 1881

Loligopsis ocellata Owen, 1881: 139, pl. 26, figs. 3-8, pl. 27.

Calliteuthis ocellata, Verrill, 1881a: 402; 1882a: 412.—Dell, 1959: 99.

Stigmatoteuthis ocellata, Pfeffer, 1912: 286.

Owen gave the name *Loligopsis ocellata* to a female specimen of approximately 105 mm ML taken in the China Sea. Verrill noted the strong similarities to his new *Calliteuthis reversa*, and placed *ocellata* in the genus *Calliteuthis*. Pfeffer, in 1912, changed the name again, putting *ocellata* into his earlier erected genus *Stigmatoteuthis*.

Despite Owen's description, which is of considerable length, and the accompanying illustrations, the details necessary for specific identification

in the family Histoteuthidae are not given. Much effort was given to locate the type, but it could not be found. Thus, I believe that this species should be designated as a *species dubia*.

The specimen misidentified by Chun (1910: 149-170) as *Calliteuthis ocellata* has been discussed earlier in this paper, under the species *Histioteuthis dofleini* Pfeffer, of which it is the type.

Histiopsis Hoylei Goodrich, 1896

Histiopsis Hoylei Goodrich, 1896: 15, pl. 4, figs. 62-71.—Hoyle, 1897: 373. *Stigmatoteuthis Hoylei*, Pfeffer, 1900: 170; 1912: 281.—Dell, 1959: 99.

Goodrich erected this species for a juvenile whose mantle measured 19 mm long ventrally. This specimen was taken near the Andaman Islands, Indian Ocean. He was uncertain of its systematic position and placed it provisionally in Hoyle's genus *Histiopsis*, but noted its close relationship to the genus *Histioteuthis*. Pfeffer, in 1900, used *Hoylei* as the type-species for his genus *Stigmatoteuthis*. In his monograph of 1912, Pfeffer elaborated on the description of *Hoylei*, but all was based on Goodrich's original description and illustrations of the unique type.

Unfortunately, Goodrich did not give the details necessary for specific identification. The type was sought in the collections of the Calcutta Museum, from whence the specimen came, but it could not be found (Dr. H. C. Ray, Zoologist, Zoological Survey of India, Calcutta, personal communication). Thus no choice is left but to consider *Histiopsis Hoylei* as a *species dubia*.

Calliteuthis (Meleagroteuthis) asteroessa Chun, 1910

Calliteuthis (Meleagroteuthis) asteroessa Chun, 1910: 170. *Meleagroteuthis asteroessa*, Pfeffer, 1912: 296.—Thiele, 1921: 451, pl. 54, figs. 15-20.—Dell, 1959: 99.

Chun (1910), in his key to the genus *Calliteuthis*, gave an incomplete description of a new species that he called *Calliteuthis (Meleagroteuthis) asteroessa*. He described *asteroessa* as differing from *meleagroteuthis* by the lack of tubercles on the arms and mantle and by the presence of fewer rows of photophores on arms I, II, and III, but as sharing with *meleagroteuthis* the character of eight rows of photophores on the fourth arms. No specimen, illustration, or locality was given.

Thiele (1921), in his report on "Die Cephalopoden der Deutschen Südpolar-Expedition 1901-1903," elaborated on Chun's description and illustrated the type, a juvenile of 11.5 mm ML. The specimen is too immature and the illustrations and description are totally inadequate for specific identification. It is impossible to tell whether this specimen is a juvenile of *meleagroteuthis* or represents a separate and new species. Considering the above discussion and the fact that the specimen could not be

located in the Berlin Museum, where most of the cephalopods from the German Southpolar Expedition are deposited, the species *asteroessa* must be considered a *species dubia* and of no more concern to the systematics of the histioteuthids.

Stigmatoteuthis japonica Pfeffer, 1912

Calliteuthis reversa Verrill, Hoyle, 1886: 183, pl. 33, figs. 12-15.

Calliteuthis ocellata (Owen), Berry, 1912a: 432 (in part).

Stigmatoteuthis japonica, Pfeffer, 1912: 284.—Sasaki, 1916: 98; 1929: 261.

Calliteuthis japonica, Dell, 1959: 100.—Taki, 1964: 290.

In his "Report on the Cephalopods Collected by the HMS *Challenger* . . .," Hoyle referred a specimen taken off Ino Sima, Japan, to *Calliteuthis reversa* Verrill. A second specimen taken off New Zealand was immature, and although Hoyle included it under *reversa*, he considered its identification as uncertain; therefore, it does not enter into the present considerations.

Hoyle noted a difference in the mantle element of the *funnel-mantle locking apparatus* in the CHALLENGER specimen and described it as being "divided into two portions, of which the posterior is much the more prominent, and separated by a distinct gap from the anterior, which is low and narrow." Hoyle illustrated one of the larger tentacular suckers as having teeth only on the posterior margin. The *gladius*, he illustrated as having the very posterior margin reflected as a membranous expansion.

Berry (1912a) referred this specimen to *Calliteuthis ocellata* (Owen). Pfeffer (1912) gave the specimen a new name, *Stigmatoteuthis japonica*. It was later noted in works of Sasaki (1916, 1929) and by Taki (1964), but all references were to the original CHALLENGER specimen, and no new material was identified to this species.

Hoyle's description and illustrations are totally inadequate. The reflected posterior margin of the gladius and the two-parted mantle cartilage could easily be artifacts of preservation; I have observed the latter case of the two-parted mantle ridge in a number of specimens belonging to several species of histioteuthids. About the only distinguishing character remaining is the armature of the enlarged tentacular suckers. Hoyle's illustration showed the teeth confined to the distal margin of the ring; this characteristic is also present in *celetaria celetaria*, described earlier in this paper. It has been seen, however, that the armature, or lack of it, on the suckers in the histioteuthids is a somewhat variable character and therefore of no value as a sole distinguishing character for a species.

The type, present in the collections of the British Museum, was examined and found to be in such poor condition, apparently from having been dried up in the past, as to render it worthless for identification purposes. On the basis of the above facts, I believe that *Stigmatoteuthis japonica* should be considered a *species dubia*.

Stigmatoteuthis Goodrichi Pfeffer, 1912

Stigmatoteuthis Goodrichi Pfeffer, 1912: 289, pl. 22, figs. 9-12.

This species was erected by Pfeffer on the basis of an arm taken in the mid-North Atlantic. The described and illustrated characters of the single arm are completely inadequate for a specific identification. Furthermore, the type, deposited in the Hamburg Museum, was destroyed in World War II. Thus, with nothing remaining to warrant the validity of this species, *Stigmatoteuthis Goodrichi* should be formally retired as a *species dubia*.

MISIDENTIFIED SPECIMENS

Calliteuthis Alessandrinii (Verany, 1847)

Loligo Alessandrinii Verany, 1847: 514; 1851: 99, pl. 35, figs. f-h.

Calliteuthis Alessandrinii, Appellöf, 1890: 27, figs. 7-11.—Hoyle, 1897: 11.

Verany gave nothing in his description of this small specimen to warrant its inclusion in the family Histiotteuthidae. The broad posterior end of the mantle and the shape of the tentacular club and its sucker arrangement are foreign to the family.

This specimen was recognized by Troschel (1857) as being an enoploteuthid, a conclusion concurred with by numerous succeeding workers. Appellöf, however, identified a small specimen in his possession with Verany's and changed the genus of *Alessandrinii* to *Calliteuthis*; hence the necessity for the present treatment of this species. Appellöf's specimen was obviously an enoploteuthid, as was Verany's.

The abbreviated synonymy refers but to its short history in the literature of the Histiotteuthidae.

Calliteuthis nevroptera Jatta, 1896

Calliteuthis nevroptera Jatta, 1896: 118, pl. 31, figs. 1-11.

Jatta described and illustrated in detail the 20-mm-ML specimen on which this species was based. It is obvious that it does not belong in the family Histiotteuthidae. It appears to be a juvenile of *Ctenopteryx siculus* (Verany, 1851), as was first recognized by Pfeffer in 1900.

Dubioteuthis physeteris Joubin, 1900

Dubioteuthis physeteris Joubin, 1900: 102, pl. 15, figs. 8-10.

Joubin named this species on the basis of a large, headless specimen recovered from a whale off the Azores. Erecting a new genus for it, *Dubioteuthis*, Joubin placed it in the subfamily Histiotteuthinae. Obviously not a histiotteuthid, *physeteris* was first recognized as belonging to *Architeuthis* by Appellöf in 1902, and there it has remained.

Histiochromius Chuni Pfeffer, 1912

Brachioteuthis juv., Chun, 1910: 202, pl. 30, figs. 2-3, pl. 31, fig. 4.

Histiochromius Chuni Pfeffer, 1912: 320.

Pfeffer, in 1912, erected a new genus, *Histiochromius*, for a juvenile specimen described and illustrated by Chun (1910) as *Brachioteuthis* juv. Pfeffer named his new species *Histiochromius Chuni*.

The whereabouts of this specimen is not known, but from the illustrations and description, it is obvious that it does not belong to the family Histioteuthidae.

MUSEUM NAMES

While working at the Zoologisk Museum in Copenhagen, my husband found two brachial crowns of histioteuthids identified by Steenstrup. One bore the label "*Histoceraeus architeuthoides* Steenstrup, Atlanterhavet, 26-6-1863, af Bergen," and the other, the label "*Histoceraeus dubius*, Steenstrup, Atlanter Havet, 19°30' NB, 26°5' VL, 1865, Andréa."

No references to these specimens have been found in the literature. But a single reference to the generic name was located (with a slight difference in spelling), and that is in a note on egg masses (Steenstrup, 1880: 109), wherein Steenstrup refers to the possible type of fry of "min *Histioceraeus*."

The names *Histoceraeus architeuthoides* and *Histoceraeus dubius* are obviously museum names and of no validity. They are mentioned here only for the sake of adding to the completeness of the present treatment of the family Histioteuthidae.

GENERAL DISCUSSION

The present study shows that the family Histioteuthidae is composed of a relatively large number of closely knit species. Though, at present, the interrelationships of the member species are not clear, it is obvious that the old breakdown of genera into *Histioteuthis*, *Calliteuthis*, *Meleagroteuthis*, and others, depending on the author, was based on inadequate knowledge of the group and should be discarded. One may dislike to retire such a popular name as *Calliteuthis*, but if no clear divisions exist in the family for defining separate genera, then there remains no choice. Considering our present knowledge, it is best that the family Histioteuthidae be considered as monotypic, with all of the species belonging to the genus *Histioteuthis*, and with that genus being redefined as given earlier in the present paper.

Such characters as the dentition of the suckers of the arms, the presence of accessory chitinous formations on the tentacular suckers, the development of the inner web, the presence of tubercles, and the concentration of the photophores, which classically have been used to define genera, are seen not to be distinctive for any one group, but are either variable in some cases, such as sucker dentition, even within a species, or are shared in

varying degrees of development with other species in varying combinations.

The development of the web transcends generic boundaries, ranging from vestigial to low, to moderate, to deep. *H. bonnellii*, historically possessing the deepest web, now shares that distinction with *macrohista*, but significantly varies from the latter species in such important features as the arrangement of the buccal membrane. A defined terminal photophore (or photophores on the arms) is no longer found to be unique, but is seen to occur in differing forms in *bonnellii*, *macrohista*, *atlantica*, *celetaria*, and *elongata*.

The concentration of the pattern of photophores respects no discrete divisions, but gradates from a widely set pattern of uniformly large organs on the ventral surface of the mantle, as in *dofleini*; to an intermixed pattern of large and small organs, as in *reversa*; to a moderately dense pattern of uniformly medium-sized organs, as in *miranda*; to a dense pattern of uniformly small organs, as in *meleagroteuthis*. Using in the same order the four preceding species, the number of rows of photophores on the fourth arms, a favorite distinguishing character used in the family, increases regularly from 3, to 4, to 5, to 8-9. Berry's species *heteropsis* shares with *meleagroteuthis* the very dense concentration of photophores, but varies sharply in the lack of the row of tubercles on the mantle and arms. In turn, the tubercles do occur in two other divergent species, *miranda*, and the yet incompletely known *bruuni*.

At least with our present knowledge, it appears that the histioteuthids are a genetically active group, displaying a diverse pattern of speciation. Whether *elongata*, with its more elongate mantle and less obviously asymmetrical eyes, might be considered more in the main line of the oegopsids or merely a unique species is conjectural. Some grouping of more closely related species is obvious in the family, even though not of generic level. Certainly, *meleagroteuthis*, *heteropsis*, and possibly *bruuni* appear to be an interrelated group; also *bonnellii* and *macrohista* have the appearance of close ancestry. The two species *reversa* and *eltaninae* are so close that they were at first considered to be subspecies until their totally different spermatophores became known. Additional material and study should also reveal to what degree divergent speciation has progressed in such widespread species as *dofleini*, *corona*, and *celetaria*. Our present material clearly indicates that discrete forms do exist, but as to whether they are of subspecific or specific level remains to be determined.

SUMARIO

MONOGRAFÍA DE LOS CEFALÓPODOS DEL ATLÁNTICO NORTE.

LA FAMILIA HISTIOTEUTHIDAE

Se revisan los mundialmente distribuidos calamares mesopelágicos de la familia Histioteuthidae. Un solo género, *Histioteuthis*, es reconocido y

redefinido. Se describen tres nuevas especies, *eltaninae*, *macrohista* y *bruuni* y una nueva sub-especie, *corona berryi*. Se designan neotipos para *miranda* (Berry, 1918), y *meleagroteuthis* (Chun, 1910) y se confirma la validez de la especie de Hoyle (1885), *atlantica*. Se da un resumen histórico amplio y la discusión taxonómica de la morfología general de la familia así como una clave de las trece especies identificadas. Cada especie es descrita e ilustrada en su totalidad y se dan sus sinonimias y distribuciones. Se discuten las *species dubia*, la publicación de especies mal identificadas y los nombres encontrados en museos.

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